SOCIAL STRUCTURE AND UNDERWATER BEHAVIOR OF HARBOR SEALS IN SOUTHERN MONTEREY BAY, CALIFORNIA

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To understand harbor seal social and mating strategies, I examined site fidelity, seasonal abundance and distribution, herd integrity, and underwater behavior of individual harbor seals in southern Monterey Bay. Individual harbor seals (n = 444) were identified by natural markings and represented greater than 80% of an estimated 520 seals within this community.

Year to year fidelity of individual harbor seals to southern Monterey Bay coastline was 84% (n = 388), and long-term associations (>2 yrs) among individuals were common (>40%). Consistent with these long-term associations, harbor seals were highly social underwater throughout the year. Underwater social behavior included three primary types: (1) visual and acoustic displays, such as vocalizing, surface splashing, and bubble-blowing; (2) playful or agonistic social behavior such as rolling, mounting, attending, and biting; and (3) signal gestures such as head-thrusting, fore-flipper scratching, and growling. Frequency of these types of behavior was related to seal age, gender, season, and resource availability. Underwater behavior had a variety of functions, including promotion of learning and social development, reduction of aggression and preservation of social bonds by maintaining social hierarchy, and facilitation of mate selection during breeding season.

Social behavior among adult males was significantly correlated with vocalization characteristics ($r = 0.99$, $\chi^2 = 37.7$, $p = 0.00087$), indicating that seals may assess their competition based on underwater vocalization displays and adopt individual strategies for attracting females during breeding season based on social status. Individual mating strategies may include defending underwater territories, using scramble tactics, and developing social alliances.

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CHAPTER 1:

INDIVIDUAL IDENTIFICATION, SITE FIDELITY, DISTRIBUTION, ABUNDANCE, AND HERD INTEGRITY

INTRODUCTION

The harbor seal (*Phoca vitulina richardsi*) lives throughout the eastern Pacific, from the Aleutian Islands, Alaska, to the San Roque Islands in Baja California (King 1983, Reeves and others 1992). Adults measure from 1.2 to 1.9 m standard length, with mass averaging 90 kg. Females are generally smaller than males. Harbor seals are characterized by individually distinct pelage patterns, varying from white, light gray to nearly black. The pelage is often counter-shaded, or darker on the dorsal surface than underbelly, and marked by irregularly shaped white and brown spotting, providing camouflage while ashore or at sea. Harbor seals principally occur near shore, resting on sand or cobble beaches, inter-tidal ledges, rocky islets, and estuarine mudflats, and foraging nocturnally along the continental shelf on benthic fishes and cephalopods (Harvey and others 1995) in ocean depths less than 100 meters (Eguchi 1998). These seals are non-migratory but may travel hundreds of kilometers in search of food or breeding habitat (King 1983, Reeves and others 1992).

Harbor seals breed during late winter, spring, or summer from February to September, depending on latitude. At the southern end of their distribution, Baja California, harbor seals breed earlier (February-April) than in northern latitudes, such as the Aleutian Islands and Alaska, where breeding occurs during late spring and summer. Along the central California coastline, pupping begins in March and ends in May, followed by mating season, which may extend into early July (King 1983, Riedman 1990, Reeves and others 1992). Mating strategy, however, is unknown. Male harbor seals produce underwater vocalizations that may function to maintain underwater territories, dominance hierarchies, or advertise breeding condition, fitness, or social status to females (Sullivan 1981, Le Boeuf 1991, Hanggi and Schusterman 1994, Thompson and others 1994, Van Parijs and others 1997). Mating behavior, however, is difficult to observe because harbor seals mate underwater and are relatively shy by nature, exhibiting a strong flight response when disturbed. This flight response may function to reduce vulnerability to predation or commercial harvest ashore and at sea. In California, harbor seals were commercially harvested for food,

pelts, and fuel until the early 1900's when the population had declined to a few hundred individuals (Barlow and others 1995).

During the last half century, harbor seal abundance has increased from a few hundred individuals to nearly 33,000 along the California coastline. This dramatic recovery is primarily the result of state and federal protection from commercial hunting, and declining fishery related mortality (Barlow and others 1995). With less human related mortality, harbor seal population in California has expanded into a wide range of littoral habitats, from remote beaches along the northern and central coast to abandoned piers and pilings within urban waterways such as San Francisco Bay. Harbor seals, therefore, exhibit less fear of humans. This decreased vigilance near humans has created opportunities to study harbor seals in their natural environment.

Information regarding individual activity patterns and range of movements between foraging, resting, and breeding areas has resulted from instrumentation of harbor seals with radio transmitters (Pitcher and McAllister 1981, Harvey 1987, Yochem and others 1987, Allen 1988, Thompson 1989). Generally, in studies using instrumentation, harbor seals with transmitters represent fewer than 2% of individuals within the entire community, and equipment remains attached and operational only a few months before natural shedding occurs during summer molt. Inferences regarding behavior, when extended to the entire community or life span of the individual, therefore, are relatively weak. Instead, long-term observations of individuals identified by natural markings may provide a more effective method of determining information regarding stability of a community through time, providing social context necessary for interpretation and understanding of individual behavior. The purpose of this study was to investigate effectiveness of identifying individuals by natural marking to determine site fidelity, seasonal abundance and distributions of individuals, and herd integrity of harbor seals off Monterey, California. This comprehensive understanding of a community is essential to address complex questions regarding function of individual behavior with respect to social and mating strategy.

I predicted that individual harbor seals could be distinguished and recognized reliably by pelage features, such as coloration and patterning. These individuals may exhibit fidelity to this study area throughout the year, and demonstrate individual preferences for specific haul-out areas. These preferences may be influenced by seasonal factors, such as food availability or breeding, or daily environmental conditions, such as tidal phase or sea state. Because southern Monterey Bay is sheltered from heavy northwest swell, peak abundance of harbor seals should occur during winter and early spring. Finally, I predicted that individuals would exhibit year to year fidelity to southern Monterey Bay, maintaining long-term associations with other members of the herd.

STUDY AREA

The central coast of California near the southern end of Monterey Bay is characterized by a rocky littoral zone and near shore rocky islets fringed sub-tidally by giant kelp (*Macrocystis pyrifera*) forests. The study area extends approximately 3 kilometers northwestward from Heritage Harbor, Monterey to Otter Point in Pacific Grove. Point Pinos shelters this coastline from northwest swells, providing near-shore habitat, such as calm seas surrounding rocky islets, suitable for resting harbor seals.

METHODS

From August 1995 to July 1996, I surveyed harbor seal resting areas within Hopkins Marine Life Refuge (HMLR) daily to monitor harbor seal abundance and acquire proficiency identifying and recognizing individuals by natural pelage markings (Fig. 2). From September 1996 to June 1997, I extended the survey range to include all near shore resting areas from Heritage Harbor to Otter Point. This study area is characterized by twelve primary resting sites (PLP, LP, BLP, WB, CV, BR, SR, MBA, PLZ, ELT, RMP, HBR; Fig. 1), which I surveyed semi-weekly during daytime low tides when seals were most likely ashore. During surveys, abundance of harbor seals at each site was determined, and recognizable individuals were identified by unique pelage markings.

Re-sight frequency or attendance of each individual was calculated by dividing number of days an individual was observed by total number of survey days. I categorized individuals as residents, non-

breeders, winterers, or breeders depending upon which months each was sighted. For example, individuals sighted during every month surveyed were considered residents; non-breeders were sighted during every month surveyed except breeding season (April or May through June).

Based on re-sight information from February to April 1997, population abundance was calculated using the Peterson mark/recapture method, assuming no immigration or emigration, with the Seber (1982) estimator.

I determined site fidelity by calculating relative frequency known seals were observed at each resting area, and compared site fidelity between genders using a t-test. To assess whether seals exhibited preference for particular rocks while ashore, I also determined fidelity to sub-sites within each resting area.

Regression analyses were used to determine effects of mean-monthly swell height and commercial fish landings on haul-out abundance within the entire study area. I assumed that fish landings provided a reasonable indicator of ocean productivity, or cephalopods and fishes available to foraging seals. Commercial fish landings were supplied by National Marine Fisheries Service (NMFS). I also used regression analyses to test daily effects of ocean swell on distribution of seals ashore by comparing mean daily wave height with proportion of seals resting ashore at Hopkins Marine Life Refuge (HMLR), a protected area where sites facing eastward are sheltered from northwest waves. Swell height measurements were recorded from National Oceanographic and Atmospheric Administration (NOAA) buoy 62042, located at the entrance of Monterey Bay.

Finally, herd integrity was measured by calculating annual re-sight frequency of individual seals from spring 1996 to spring 1997, and by comparing group composition within each resting sub-site throughout the duration of study using SOCPROG (Whitehead 1999), a program designed to assess social organization or duration of social relationships among individual animals. I determined whether this community consisted of individuals that associated constantly, casually, or transiently by calculating overall frequency of associations maintained through time. Prevalence of long term social relationships among individual seals was determined from the rate of re-association after more than one year.

RESULTS

During shore surveys from August 1995 to July 1997, 444 individuals (190 adult females, 100 adult males, 93 sub-adult females, and 66 sub-adult males) were identified by unique pelage patterns and re-sighted a minimum of three days (MAX = 312; Fig. 3, 4). Mean re-sight frequency of recognizable individuals was 34% or 21.3 (SE = 0.66, MAX = 57, n = 422) of 62 surveys days from September 1996 to December 1997 (Fig. 5). Among adults and sub-adults, 65% of individuals were residents who remained during the entire study, 17% disappeared or died, 14% were non-breeders. The remaining seals were winterers (<2%), transients (<2%), and breeders (1%).

During spring 1997, population size using mark recapture methods based on re-sightings of recognizable individuals, was estimated as 520 seals (95% confidence interval: LL 478, UL 561): 200 adult females (95% confidence interval: LL 189, UL 210), 80 adult males (95% confidence interval: LL 76, UL 82), 175 sub-adults (95% confidence interval: LL 147, UL 217). The remaining seals were yearlings or juveniles.

Adult harbor seals exhibited individual preferences for resting areas by using one or two primary haul-out sites. Fifty-nine percent (SE = 1.2, n = 184; Fig. 6a) of an individual's sightings were at one haul-out location. Individual site fidelity, however, was highly variable, ranging from 98 to 26% at the primary resting site. Adult males were more faithful to primary sites than adult females (65% vs. 55%, p = 0.001)

Individuals also exhibited preferences for sub-sites within primary resting areas. Thirty-five percent (SE = 1.0, Fig. 6b) of an individual's sightings were at one sub-site within a larger haul-out location. Again, individual harbor seals exhibited a wide range of daily fidelity (80 to 12%) to a specific sub-site.

From September 1996 to June 1997, mean low-tide haul-out abundance of harbor seals was 226 ± 9.1 SE (MAX = 357, n = 58). Peak abundance occurred during winter months (Fig. 7), and was significantly correlated with swell height (r = 0.87; Fig. 8a) and commercial fish landings (r = 0.82; Fig. 8b).

Harbor seals rested ashore on rocky islets along the coastline from Otter Point to Heritage Harbor (Fig. 1). The majority (64.2%, SE = 2.7, n = 58) of seals hauled out in Hopkins Marine Life Refuge (WB, CV, BR, SR; Fig. 9a, 9b); however, the proportion of seals resting ashore inside the refuge was highly variable, ranging from 0.22 to 0.97, but significantly related to season ($X^2 = 82.6$, $p << 0.01$, n = 57; Fig. 9b and c) and correlated with swell height ($r = 0.75$, $p << 0.01$, n = 54; Fig. 10).

Individual harbor seals exhibited fidelity to the study area from year to year. Eighty-three percent (83%) of identified individuals observed during 1996 also were seen in the study area during 1997 (n = 388). Seventeen percent (17%) of the population, therefore, either died or emigrated. Yearly disappearance rates of individuals from the community differed among age and gender classes. Adult females were most frequently observed from one year to the next (0.92, n = 178), followed by adult males (0.80, n = 88), sub-adult females (0.76, n = 78), and sub-adult males (0.70, n = 44).

Temporal analysis of group associations among identified individuals resting ashore together within sub-sites throughout the two years spanning 1996-1997 indicated that social organization of this community may be characterized by constant, casual, and transient associations among individual harbor seals (Fig.11). The mean association rate of individual seals drops to 0.6 during extremely short time lags of less than a few days (rapid disassociation), then decreases gradually over time lags from a few to 200 days (casual associations), and levels near 0.4 throughout the duration of study (constant companions, Whitehead 1995); therefore, 40% of associations were transient, 20% were casual, and 40% were constant or long term, continuing throughout the duration of study.

DISCUSSION

Four hundred and forty-four individual harbor seals were identified and recognized by unique pelage markings during surveys from shore; therefore, recognizable individuals represented greater than 80% of the estimated 520 seals within this community. This estimate of community size, which was based on re-sightings of individuals, was reliable considering 95% confidence intervals were within eight percent (8%), or 42, of 520 harbor seals. Identification of individuals using natural pelage patterns, therefore, may

be an effective method for monitoring harbor seal communities. This method, however, has several limitations. Identification of seals resting ashore depends upon observing seals before their pelage muddies or accumulates sand. Herds occupying estuarine or sandy coastal habitat, therefore, may be more difficult to monitor than communities of harbor seals along rocky shorelines, such as southern Monterey Bay. Coat condition of individuals also naturally declines and contrasting markings, either white or black, fade during continuous exposure to salt water and sunlight; therefore, seals may be more difficult to recognize during late spring and summer, before molting restores their pelage. Pelage of juveniles is especially susceptible to this weathering, which transforms black and white spotted coats into dull brown by September, nearly ten months before a their first molt. Juveniles, therefore, are nearly impossible to recognize by pelage markings alone. To enhance probability of recognizing individuals, therefore, I focused upon identifying individual adults and sub-adults rather than juveniles, and conducted surveys during fall, winter, and spring before their coat condition deteriorated after mating season and during summer molting.

Based upon these efforts, individual attendance, ranging from 5 to 86%, was comparable to attendance patterns of radio-tagged individuals in other studies (16 to 80%, Pitcher and McAllister 1981; 0 to 100%, Harvey 1987; 4 to 75%, Yochem and others 1987; 0 to 100%, Allen 1988; 17 to 43%, Thompson 1989). These wide ranges of attendance are primarily the result of monitoring effort, months surveyed, and individual seal behavior. Seals exhibited a wide range of fidelity to resting areas, depending on whether individuals remained in an area year-round as residents, or seasonally as breeders or winterers, or temporarily as transients or nonresidents en route between wintering and breeding habitat. The majority of adult harbor seals in this study were residents, or present during each month of study subsequent to identification. Non-breeders, who remained in southern Monterey bay during fall, winter, and early spring but departed during breeding and molting, also were common (M54, M55, M57, M73, F42, F45, F61 and others). Breeders, which were present only mid-April through the end of June, were uncommon (M78).

Harbor seals also may exhibit finer scale fidelity by preferring one or two primary resting sites along an entire coastline, embayment, or estuary (Sullivan 1979, Pitcher and McAllister 1981, Brown and

Mate 1983, Harvey 1987, Allen 1988). Individual preferences for a primary resting area were highly variable, ranging from 26 to 98%, therefore; some individuals were predictably located when resting ashore, while others exhibited more flexible haul-out behavior. Swell height influenced distribution of seals among exposed and protected resting sites; therefore, individual differences in site fidelity may relate to accessibility of preferred haul-out areas during extreme sea states or low tidal phases. Fidelity to primary resting areas also was influenced by gender. Adult males exhibited greater fidelity to resting areas than adult females, possibly by preferring resting areas higher in the supra-littoral zone and less affected by ocean conditions. Females also exhibited changing preferences for resting area related to breeding activities such as birthing and nursing young.

In contrast to studies along southern California Channel Islands (Yochem and others 1987), central Oregon coastline (Harvey 1987), Orkney Scotland (Thompson 1987), and northern California Drakes Estero embayment (Allen 1988), harbor seals rested ashore in greater abundance during late winter and early spring (February and March) than during spring breeding season (April and May) and summer molt (June and July). This difference in peak abundance may have resulted from individual preferences for breeding sites, distribution or availability of prey resources, and topographical features unique to Monterey Peninsula. Monterey Peninsula is predominantly a rocky inter-tidal coastline littered with supra-littoral rocky islets; therefore, resting habitat is ephemeral, influenced by tidal phase and sea state. During winters with severe ocean swell, the northeastern coastline of Point Pinos, especially HMLR, is relatively sheltered and protected from human disturbance, providing essential resting habitat for harbor seals unable to access sites along the open coast. As a result, harbor seals aggregated among these protected sites during heavy winter surf, then dispersed along the open coastline among exposed rocky islets when the ocean was calmer during summer and fall. Harbor seals also were more abundant ashore during months when prey, indicated by California fish landings, were plentiful, presumably because seals spend more time ashore and less time foraging at sea when resources are abundant. Seasonal declines in abundance during early breeding in late spring related primarily to movements of individuals (mostly adult females) to preferred breeding habitat

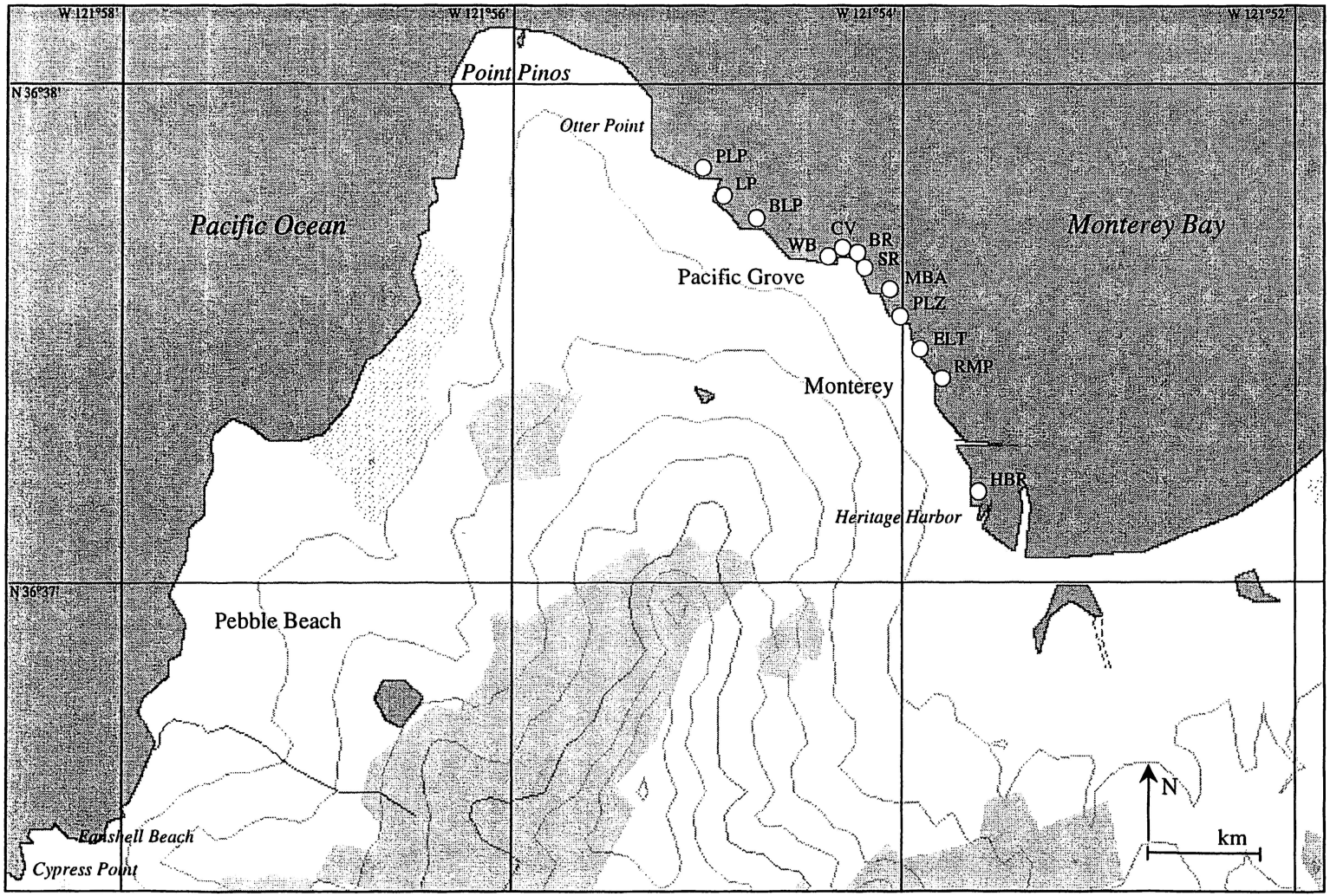
along the Pebble beach coastline (Fig. 1), which is characterized by sandy beaches inaccessible to the public and suitable for females with nursing pups.

Year to year fidelity of adult males and females to southern Monterey Bay coastline was greater than estimated survival rates for harbor seals (0.70 - 0.75; Biggs 1969, Pitcher 1977, Boulva and McLaren 1979), indicating that emigration was rare and long-term absence, greater than one year, may represent mortality. Frequency of re-association among seals through time, when compared with standard models provided by Whitehead (1999), indicated that harbor seals form constant, casual, and transient associations, which is expected within a herd consisting of resident, wintering, breeding, and nonresident seals. Forty percent of associations, however, extended throughout the duration of study, indicating that long-term associations among individuals were common. No other study has documented these comprehensive trends in harbor seal herd structure and stability.

CONCLUSION

Identification of individuals using natural pelage patterns was an effective means of characterizing and monitoring the stability of this harbor seal community. Individuals within this community represented all gender and age classes, demonstrated individual preferences for resting areas, exhibited predictable patterns in haul-out abundance and distribution, remained in the study area during consecutive seasons and years, and formed group associations that persisted for years. Information regarding the entire community was essential for understanding social context of underwater social behavior to address questions regarding function of individual behavior with respect to social and mating strategy, which is the primary focus of the following two chapters.

Figure 1. Harbor seals were observed from Otter Point to Heritage Harbor in Monterey Bay, California at 12 primary shore resting sites (PLP, Past Lover's Point; LP, Lover's Point; BLP, Before Lover's Point; WB, West Beach; CV, Cove; BR, Bird Rock; SR, Seal Rock; MBA, Monterey Bay Aquarium; PLZ, Plaza; ELT, El Torito; RMP, Ramp; and HBR, Harbor).


W 121°58'
W 121°56'
W 121°54'
W 121°52'
N 36°38'
N 36°37'
Point Pinos
Otter Point
PLP
LP
BLP
CV
BR
WB
SR
MBA
PLZ
ELT
RMP
HBR
Pacific Ocean
Monterey Bay
Pacific Grove
Monterey
Heritage Harbor
Pebble Beach
Carmel Beach
Cypress Point
N
km

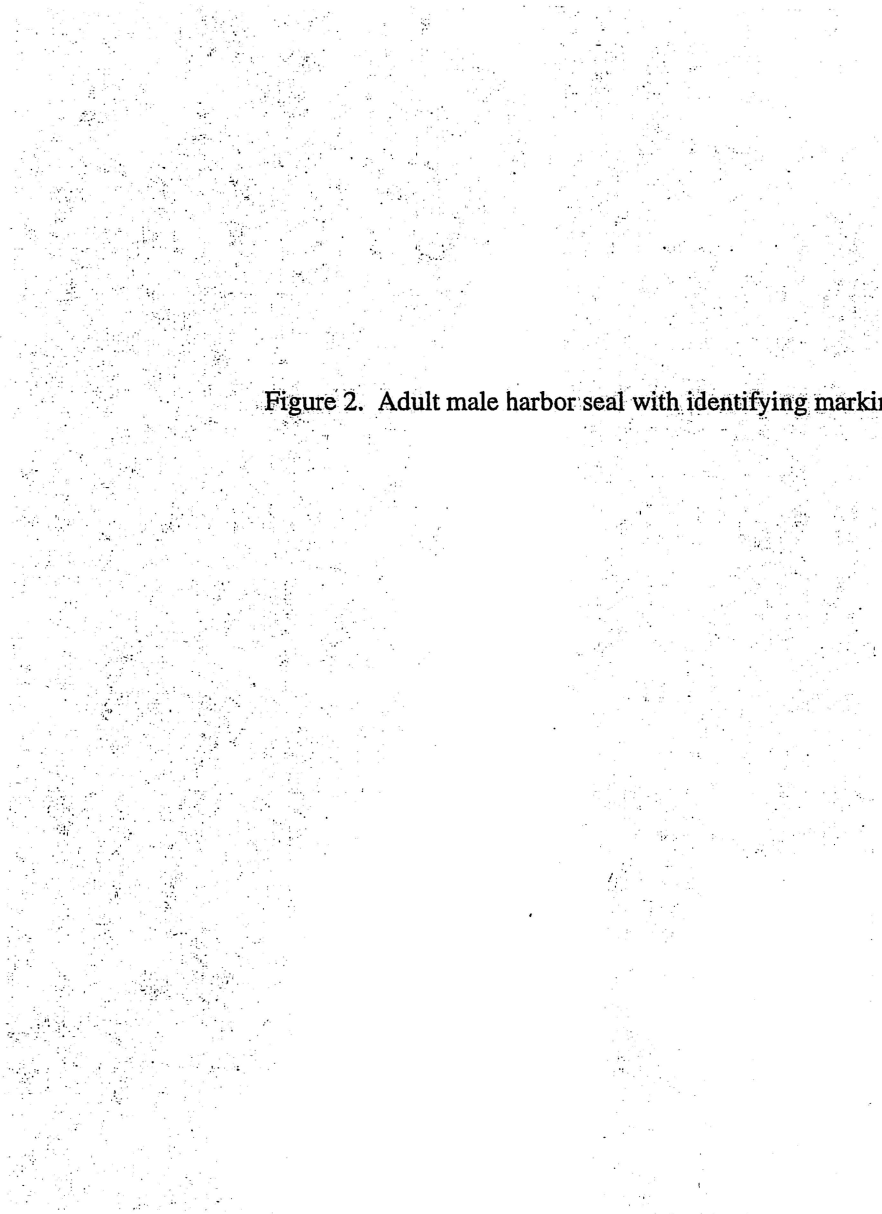


Figure 2. Adult male harbor seal with identifying markings.

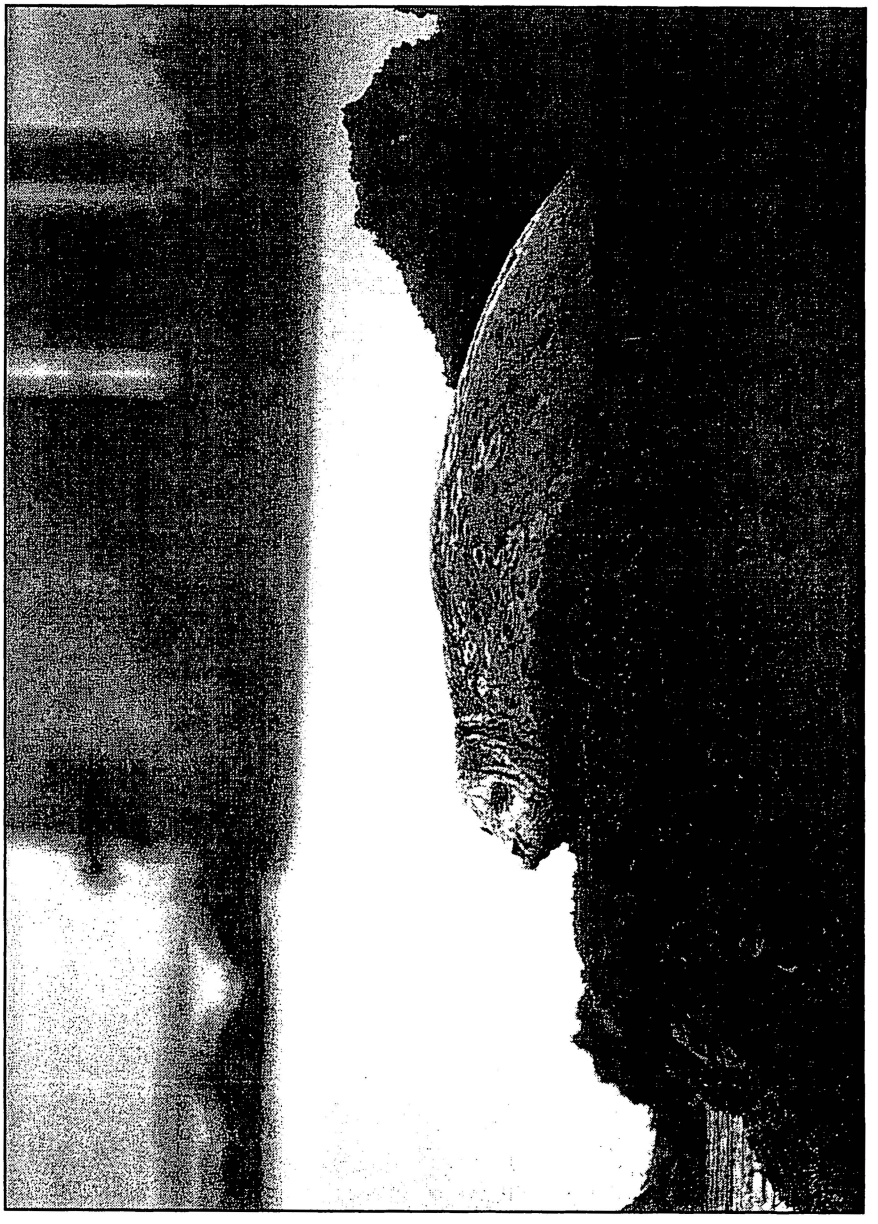
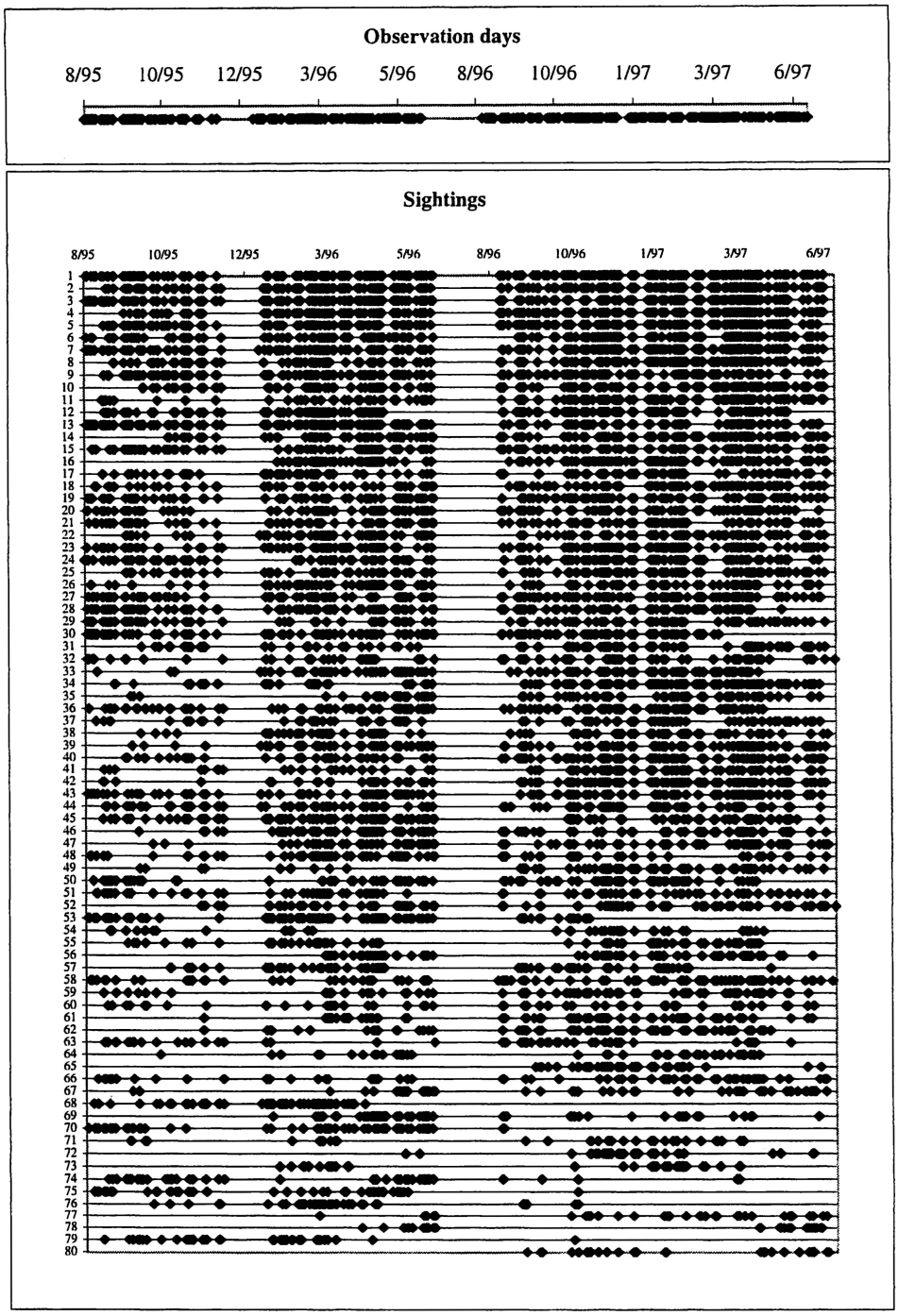


Figure 3. Dates when seals were observed and dates when 80 adult males were sighted from August 1995 through June 1997.


Observation days
8/95
10/95
12/95
3/96
5/96
8/96
10/96
1/97
3/97
6/97
Sightings
8/95
10/95
12/95
3/96
5/96
8/96
10/96
1/97
3/97
6/97
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
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80

Figure 4. Dates when seals were observed and dates when 80 adult females were sighted from August 1995 through June 1997.

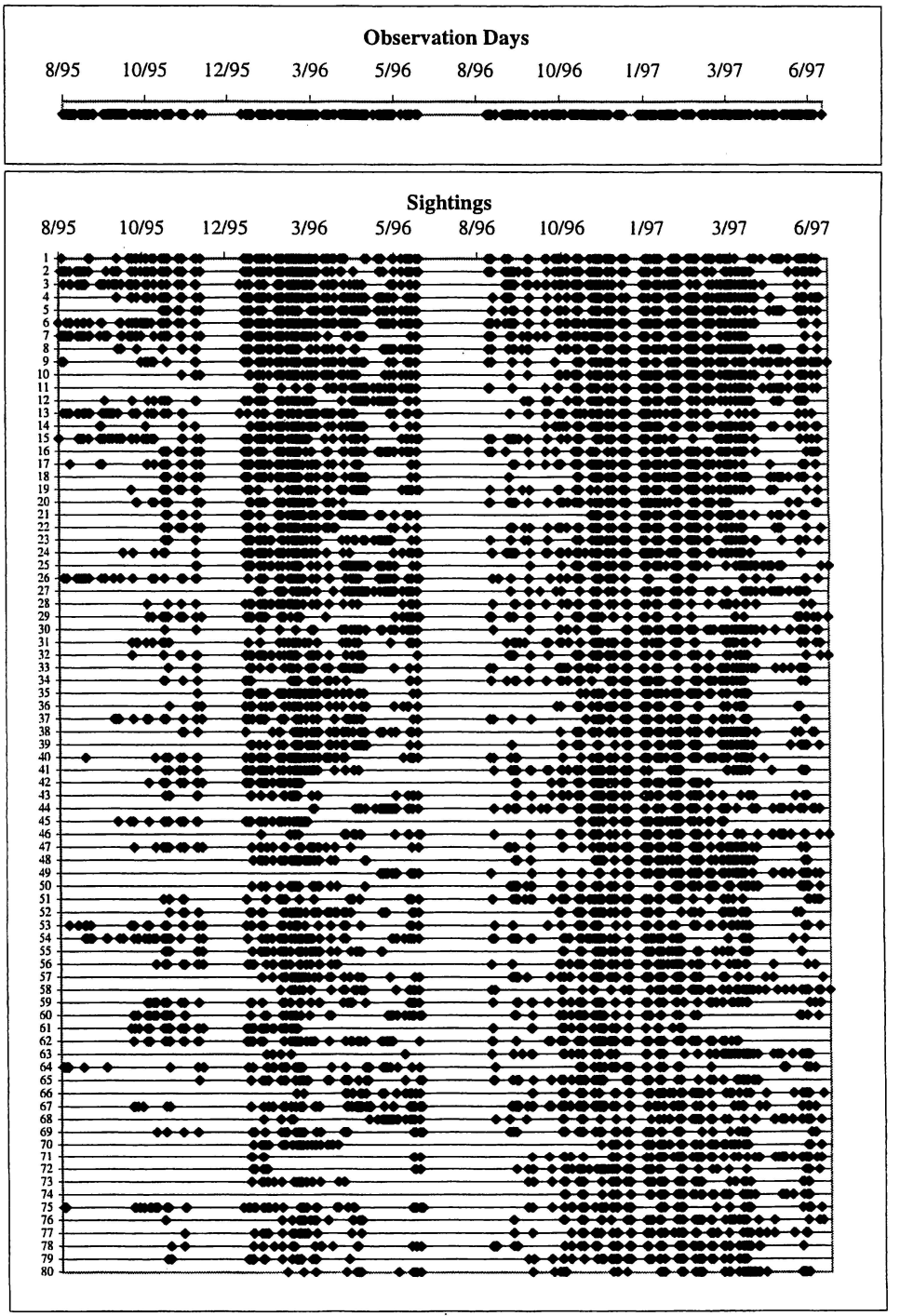

Observation Days
8/95
10/95
12/95
3/96
5/96
8/96
10/96
1/97
3/97
6/97
Sightings
8/95
10/95
12/95
3/96
5/96
8/96
10/96
1/97
3/97
6/97

Figure 5. Histogram of percent attendance or re-sighting of 423 individuals during 62 surveys of all resting areas.

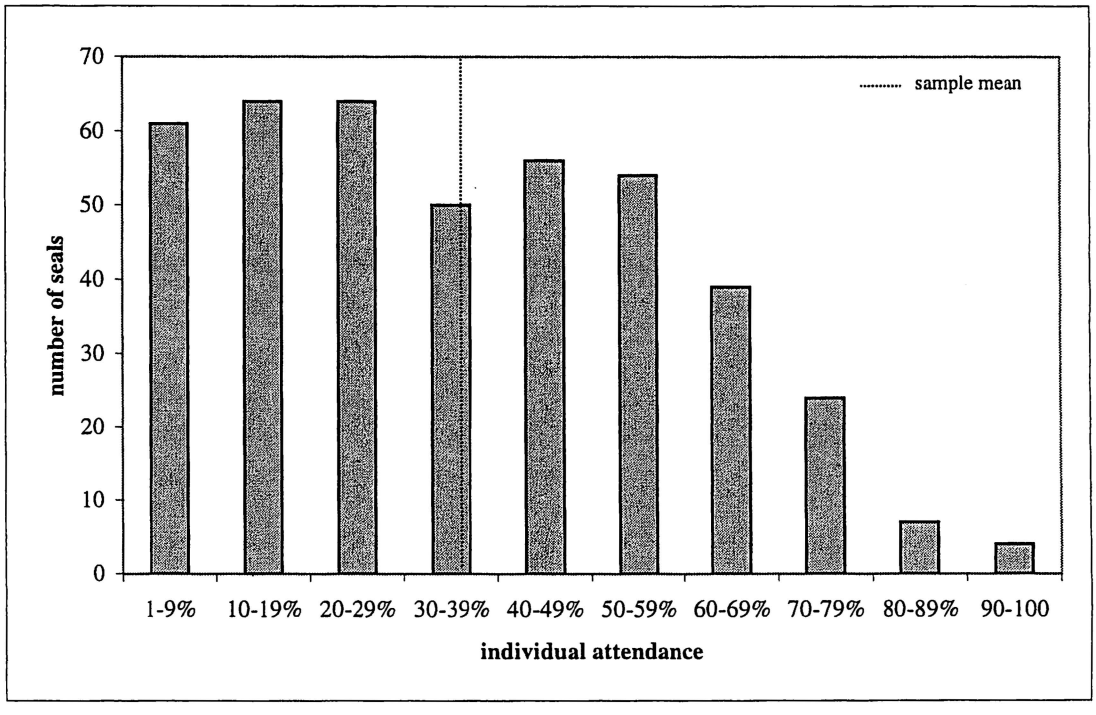
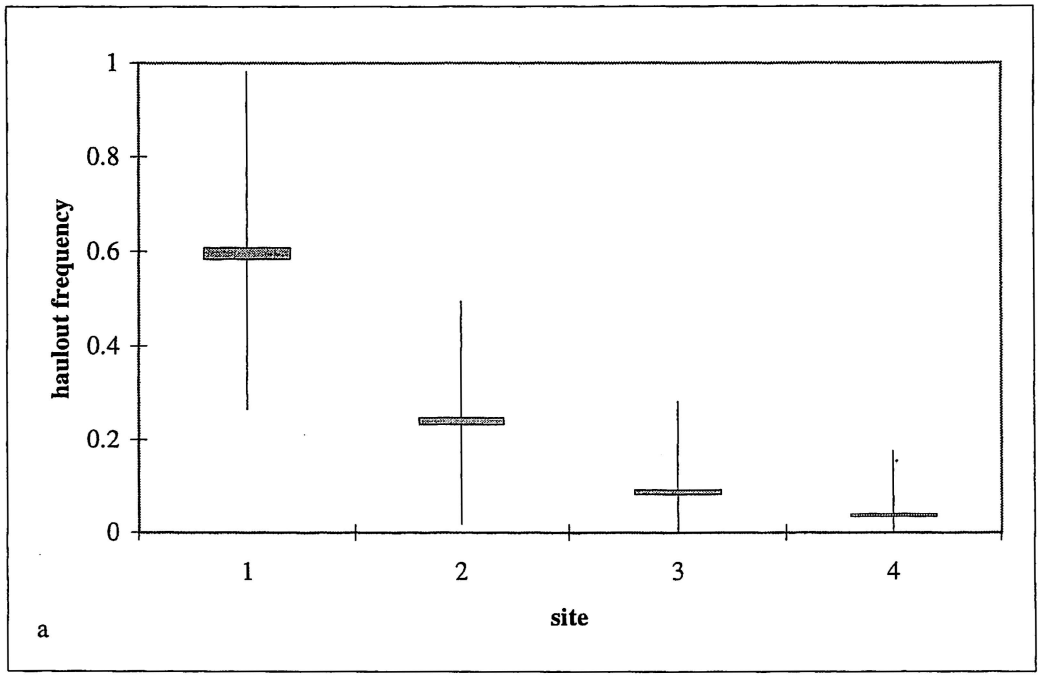

70
60
50
40
30
20
10
0
number of seals
sample mean
1-9%
10-19%
20-29%
30-39%
40-49%
50-59%
60-69%
70-79%
80-89%
90-100
individual attendance

Figure 6. Haul-out frequency (mean ± SE boxes, and range) of individual seals (N = 184) at their primary, secondary, tertiary, and quaternary (a) sites, and (b) sub-sites.


haulout frequency
1
0.8
0.6
0.4
0.2
0
1
2
3
4
site
a

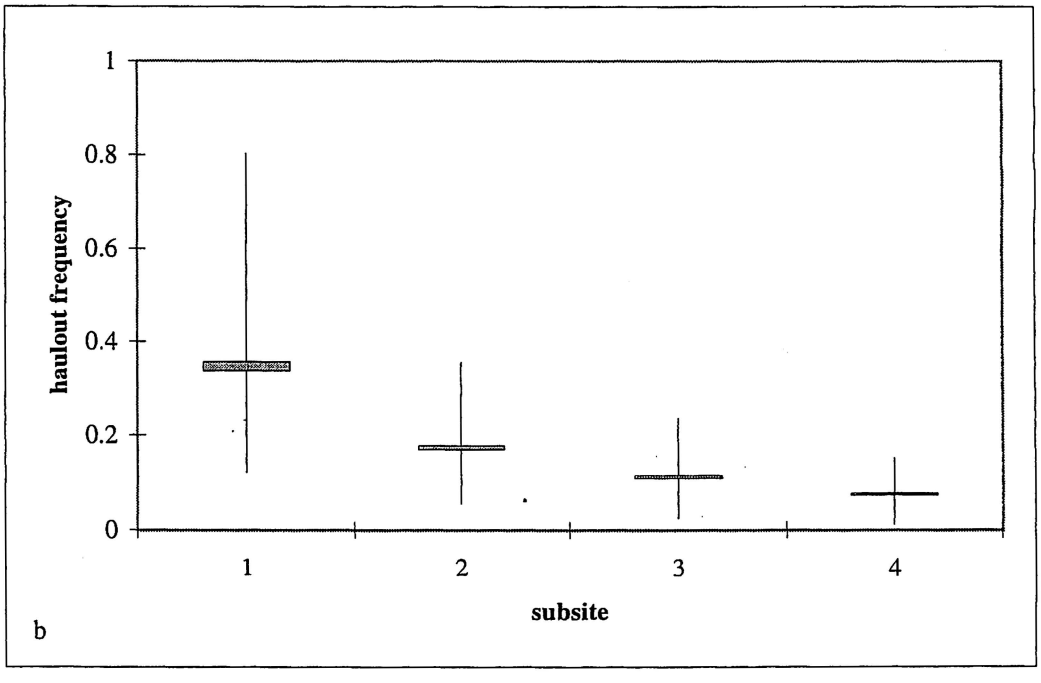

haulout frequency
1
0.8
0.6
0.4
0.2
0
1
2
3
4
subsite
b

Figure 7. Total counts of harbor seals among all 12 resting sites from August 1996 to July 1997.

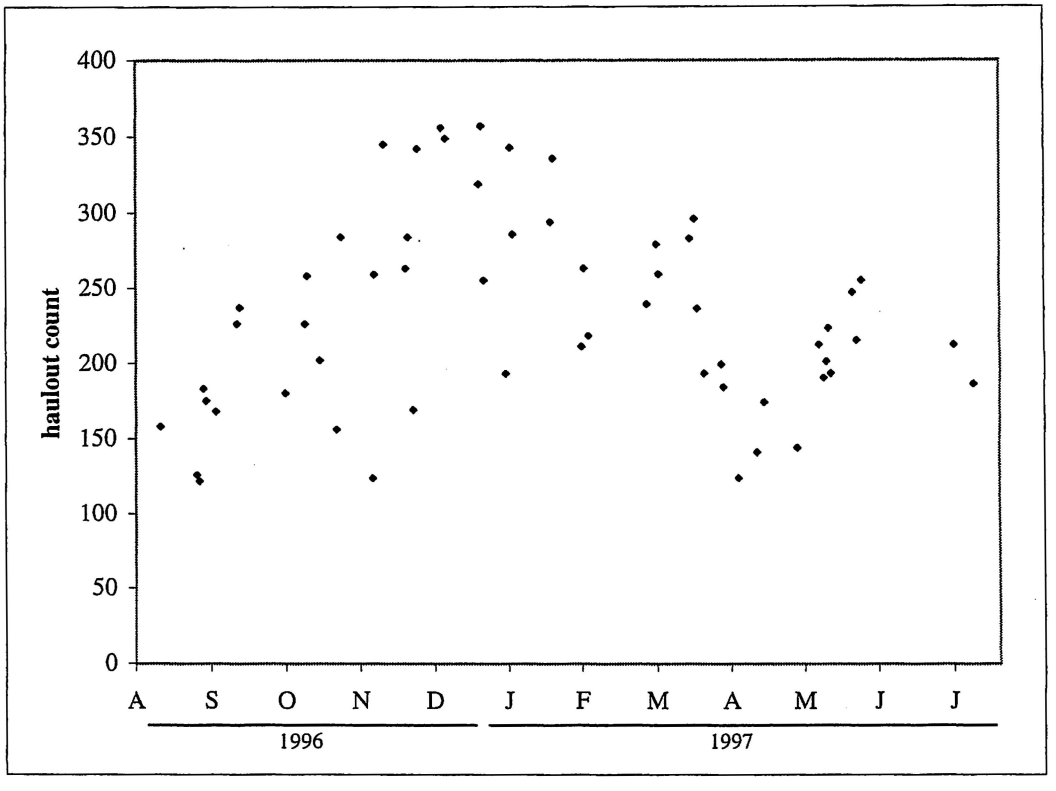
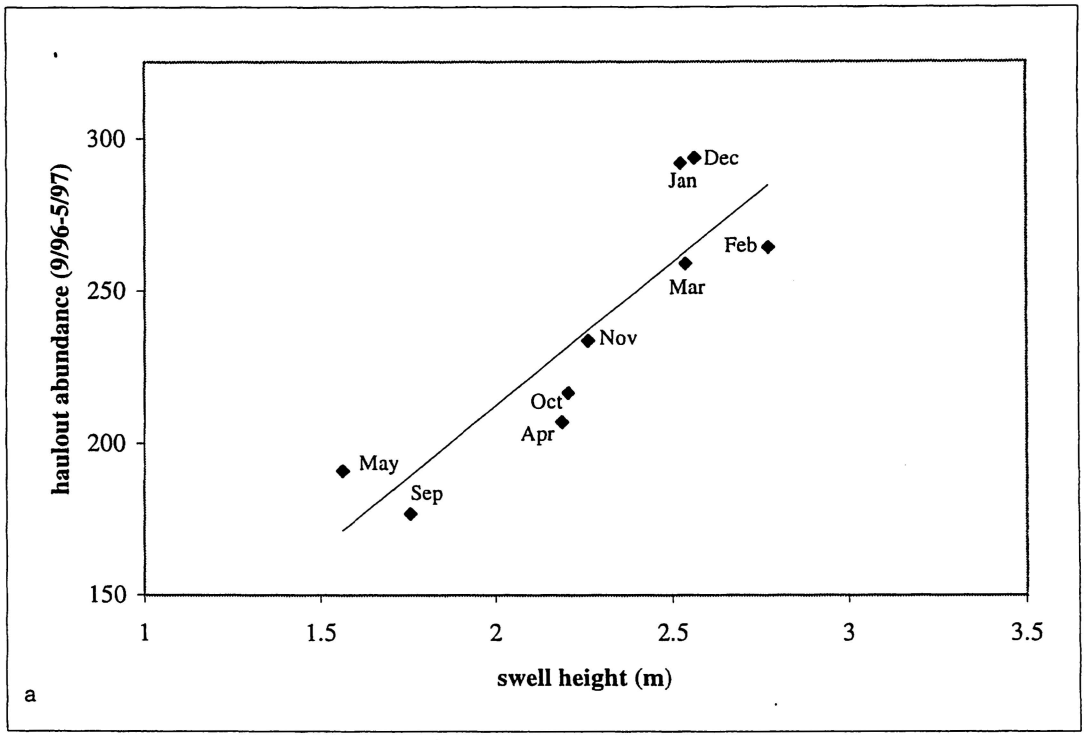

haulout count
400
350
300
250
200
150
100
50
0
A
S
O
N
D
J
F
M
A
M
J
J
1996
1997

Figure 8. Mean monthly haul-out abundance compared with (a) mean monthly swell height and (b) mean monthly California fish landings.


haulout abundance (9/96-5/97)
300
250
200
150
1
1.5
2
2.5
3
3.5
swell height (m)
Dec
Jan
Feb
Mar
Nov
Oct
Apr
May
Sep
a

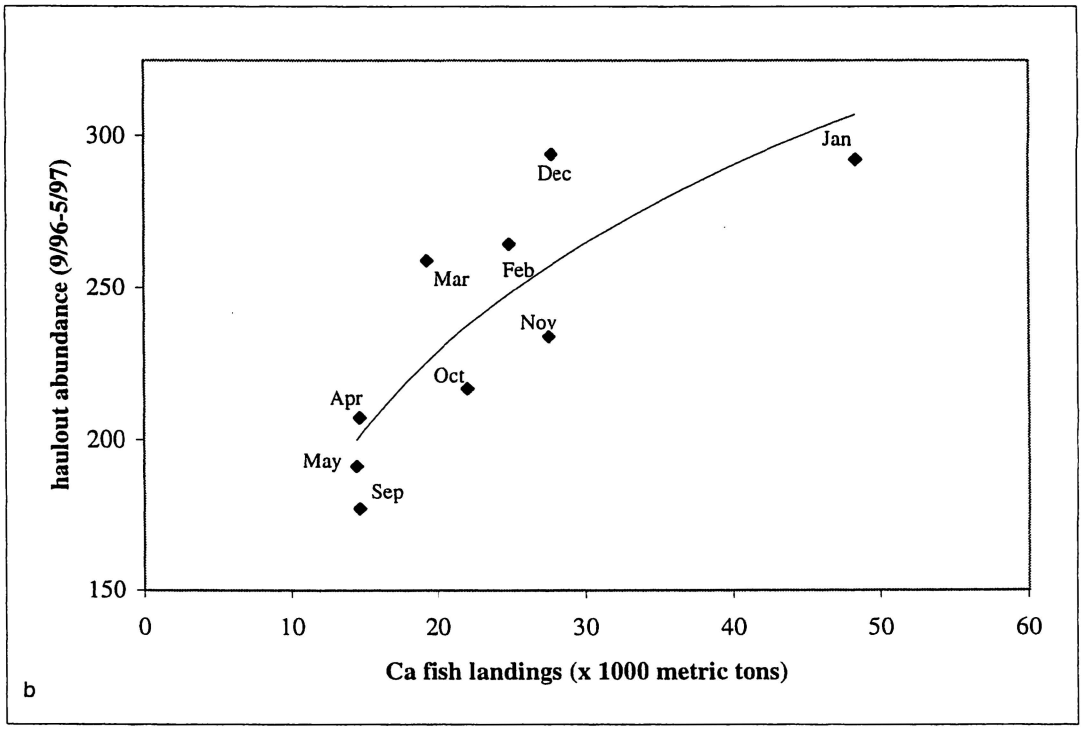

haulout abundance (9/96-5/97)
300
250
200
150
0
10
20
30
40
50
60
Ca fish landings (x 1000 metric tons)
Jan
Dec
Mar
Feb
Nov
Oct
Apr
May
Sep
b

Figure 9. Total counts of harbor seals resting ashore in Hopkins Marine Life Refuge (HMLR, sites WB, CV, BR, and SR; light 'x's) from August 1995 to July 1997, and total counts among all 12 resting sites from August 1996 to July 1997, dark circles (a); mean haul-out frequency (± SE) at each of the 12 resting areas surveyed during winter / spring (November 1996 to April 1997, b), and summer / fall (August to October 1996, May to July 1997, c).

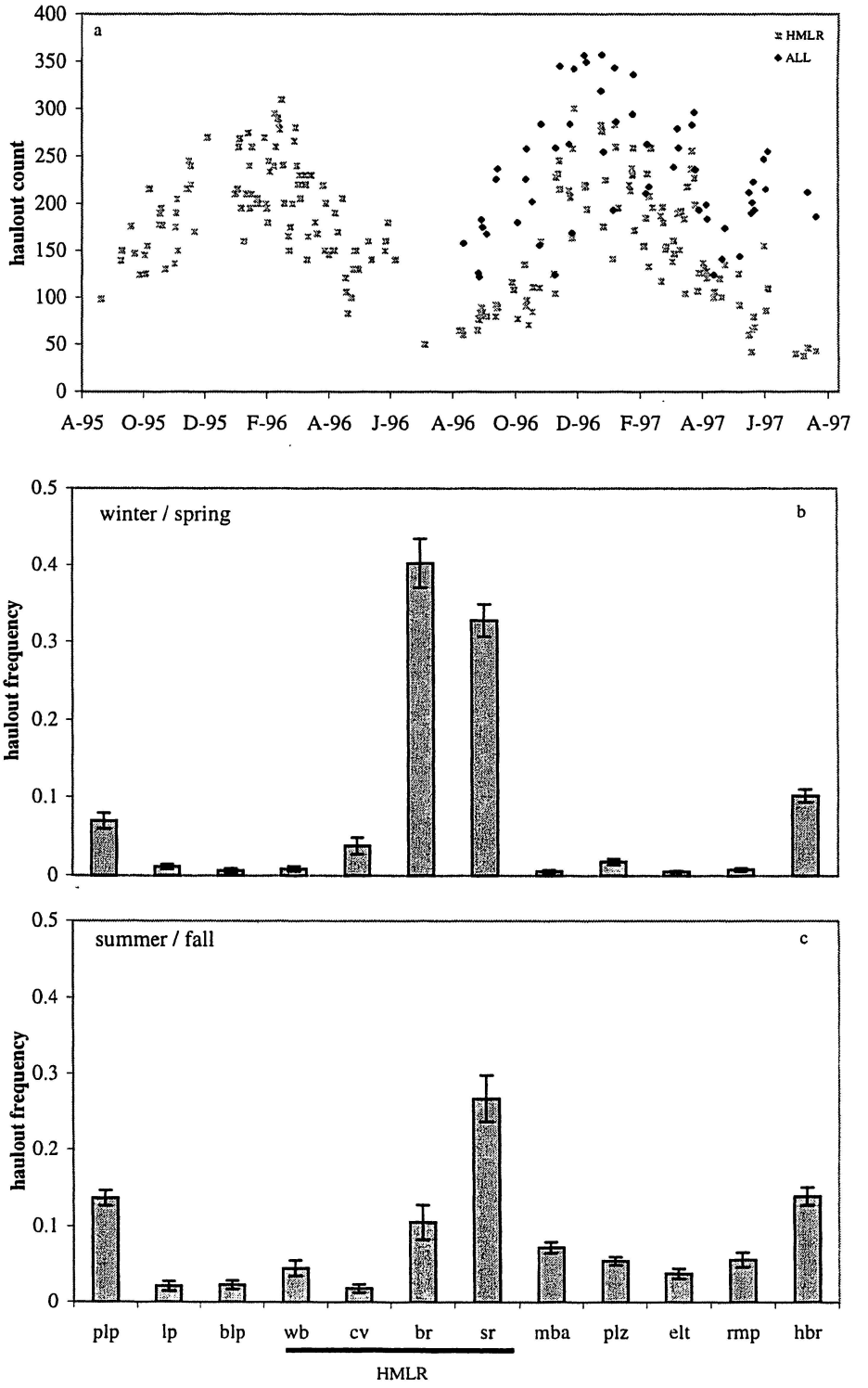

a
HMLR
ALL
haulout count
400
350
300
250
200
150
100
50
0
A-95
O-95
D-95
F-96
A-96
J-96
A-96
O-96
D-96
F-97
A-97
J-97
A-97
b
winter / spring
haulout frequency
0.5
0.4
0.3
0.2
0.1
0
c
summer / fall
haulout frequency
0.5
0.4
0.3
0.2
0.1
0
plp
lp
blp
wb
cv
br
sr
mba
plz
elt
rmp
hbr
HMLR

Figure 10. Proportion of total seals resting ashore within HMLR during low tide compared with swell height (m).

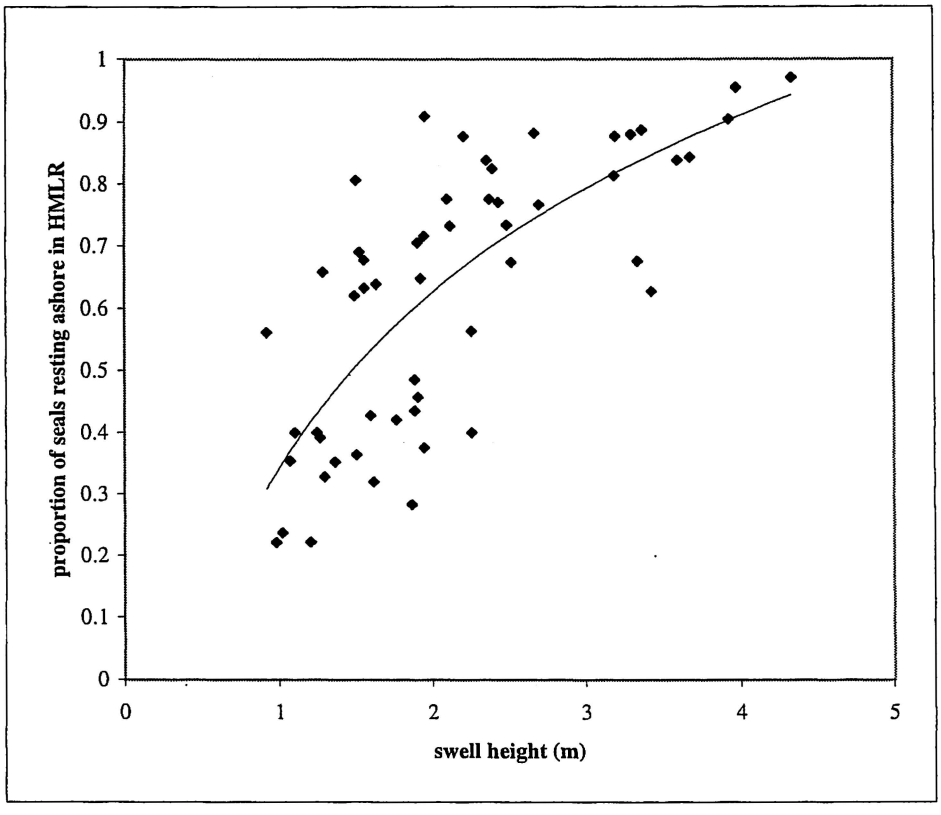
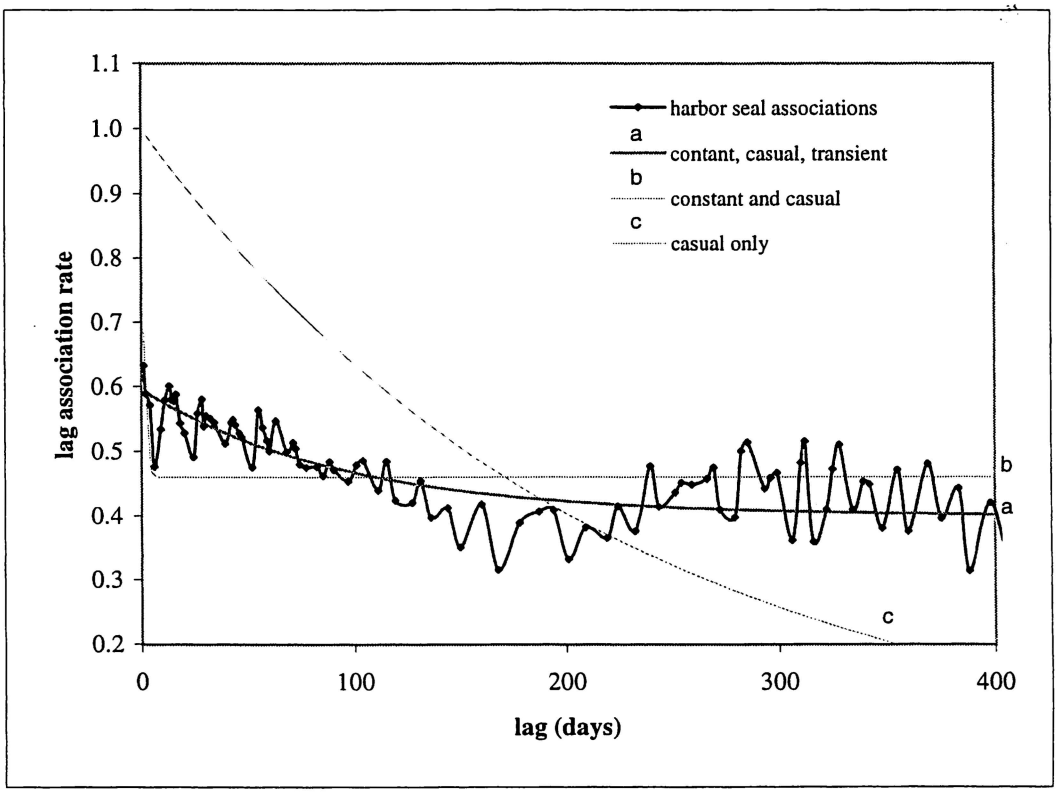

proportion of seals resting ashore in HMLR
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
1
2
3
4
5
swell height (m)

Figure 11. Mean re-association rate individual seals within shore sub-sites during time intervals from 1 to 400 days.


1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
lag association rate
0
100
200
300
400
lag (days)
harbor seal associations
a
contant, casual, transient
b
constant and casual
c
casual only
b
a
c

CHAPTER 2:

UNDERWATER BEHAVIOR

INTRODUCTION

Social behavior has a variety of essential functions: reinforcing social bonds necessary for cooperative hunting or protection from predation, reducing aggression or stress among individuals within social groups, facilitating mate selection, and promoting social development of young (Bekoff 1972, Ehrlich and Roughgarden 1987). These behaviors increase survival and reproductive success of individual animals within a social community. Individuals exhibit social behavior specific to social and gender class, and dependent upon distribution and abundance of resources such as food, shelter, and mates (Ehrlich and Roughgarden 1987). For example, adult males must often compete with other males for mating privileges, females require resources to raise young, and young need to mature developmentally and socially. When resources are scarce, competition intensifies and social behavior is limited to satisfying essential requirements such as obtaining food and mates. In contrast, when resources are plentiful, competition is reduced and energy is expendable for non-essential social behaviors such as play (Bekoff 1972, Ehrlich and Roughgarden 1987). An understanding of social behavior, therefore, is crucial for determining whether and how animals survive and reproduce, and how environmental factors may alter these processes.

Pinniped social behavior primarily has been studied among seals that aggregate ashore while breeding or mating. During breeding and mating, otariids (e.g. California sea lion, *Zalophus californianus*; Northern fur seal, *Callorhinus ursinus*) and phocids (e.g. elephant seal, *Mirounga* sp.; weddell seal, *Leptonychotes weddelli*) form seasonal breeding colonies where males obtain mating privileges by defending females or breeding habitat required by females (Bartholomew 1970, Boness 1991, Le Boeuf 1991). After breeding, however, these pinnipeds migrate or disperse widely to forage. Other phocids, such as the harp seal (*Phoca groenlandicus*), bearded seal (*Erignathini barbatus*), and ringed seal (*Phoca hispida*) mate underwater. These seals have adapted to changing ice conditions in extreme latitudes by dispersing widely during breeding to use available ice for pupping, and during winter to access feeding resources (Riedman 1990). Year-round social behavior of most pinnipeds, therefore, is inherently difficult to observe and study.

In contrast, the Pacific harbor seal (*Phoca vitulina richardsi*) lives in a temperate ocean with mild seasonal variability where food resources are relatively constant and migration is rare. During resting and breeding, harbor seals are gregarious on shore, forming herds that fluctuate daily relative to environmental conditions such as tide level, time of day, weather, and food availability (Slater and Markowitz 1983, Brown and Mate 1983, Stewart 1984, Allen and others 1984, Harvey 1987, Thompson 1987). Seasonally and annually, however, herds may represent stable social communities (Nicholson, unpubl. data). Harbor seals, therefore, provide an opportunity to study social behavior year-round and determine how these behaviors relate to survival and reproductive success.

Although social interactions on shore within these herds are infrequent, brief, and primarily represent competition for resting space (Sullivan 1982, Davis and Renouf 1987, Godsell 1988), harbor seals exhibit a complex and dynamic repertoire of underwater social behaviors near these resting sites. Underwater social behavior exhibited by harbor seals includes lob-tail and fore-flipper splashing, paired somersaulting and mounting, porpoising, bubble-blowing, and vocalizing (Venables and Venables 1957, Bishop 1968, Wilson 1978, Sullivan 1981, Renouf and Lawson 1986, Hanggi and Schusterman 1994). These types of behavior may function to maintain social relationships, underwater territories, or leks, or merely represent play among juveniles (Bishop 1968, Wilson 1978, Sullivan 1981, Renouf and Lawson 1986, Hanggi and Schusterman 1994). I studied underwater social behavior among well-known individual seals, representing all gender and social classes, during years with varying environmental stress and food availability, to understand the underwater social nature of harbor seals and provide insights regarding factors that affect their survival and reproductive success.

Specifically, I described underwater behavior, compared behavioral activity throughout the year, related differences in frequency of specific types of behavior among gender and social classes, determined how these kinds of behavior were related by examining two-step sequences, compared activity among years with varying environmental stress, and examined significance of types of behavior regarding social and mating strategy.

I predicted that harbor seals were highly social mammals that exhibited a complex repertoire of social behavior. Individuals exhibit underwater social behavior year-round, maintaining social contact with other seals in the herd during summer, fall, winter and mating season.

I also predicted that harbor seals exhibit underwater social behavior specific to social class, which reflects social status, reproductive strategy, and physiological or social development. For example, seals may exhibit social behavior that reduces or helps manage aggression within social groups, indicating social hierarchy. In addition, males may perform more overt or display behavior than females, reflecting sexual selection for male advertisement or competition among males for estrous females. Males may perform more complex or intense underwater vocalizations than sub-adult males, which may reflect physical or developmental capabilities. Adult females may rest more than other social classes to conserve energy resources required for nurturing and raising healthy pups.

Behavioral sequences should be predictable, reflecting communication of social disposition or status. In addition, I predicted that seasonal or annual variation in social activity should be related to availability of resources or environmental stress.

METHODS

From August 1996 to June 1997, I recorded underwater behavior of individual seals using a housed video camera while free-diving. Individual seals were identified by unique color pattern in their pelage. During underwater sessions, I used focal animal sampling (Altmann 1974), recording behavior of each individual for a maximum of ten minutes. Observations also were recorded opportunistically or *ad libitum* when non-focal seals were interacting with focal seals (Altmann 1974). To maximize and standardize my ability to view underwater behavior, I conducted dives during daylight hours, mid to high tide, light to moderate swell (<2 meters) with underwater visibility greater than two meters.

I determined daily number of adult male seals performing social behaviors such as underwater vocalizing, paired-somersaulting or rolling, and mounting, during fall (September, October, November), winter (December, January, February), and spring (March, April, May). Seasonal data were tested for

homoscedasticity and normality. When these assumptions were met, or could be met by transformation of data, seasonal means were compared using ANOVA and Tukey's HSD (Spjotvoll/Stoline) post hoc comparison test to determine whether seals were socially active throughout the year, and in which seasons behavior differed. Otherwise, seasonal means were compared using nonparametric ANOVA or Kruskal-Wallis test, and the Games and Howell method for unplanned pairwise comparisons.

Relative numbers of bouts of each behavior were determined for each of three social classes: adult males, sub-adult males, and sub-adult females. By using a contingency table, I determined whether behavior depended upon social class. ANOVA and Tukey's HSD (Spjotvoll/Stoline) post hoc comparison tests were used to determine differences in mean bout duration among social classes. Data were tested for normality and homoscedasticity, and transformed to satisfy these assumptions when necessary. I also analyzed two-step sequences in behavior, or the frequency in which a behavior followed another, using contingency tables to determine whether behavioral sequences among social classes were predictable.

I performed correlation and factor analysis on the relative frequency of each behavior for fifteen well-known individuals (nine adult males, three sub-adult males, and three sub-adult females) to determine whether social class could be predicted based on behavior, and what behavior was significant to this prediction. Behavioral differences were investigated further by comparing mean factor scores between (1) adult males and sub-adults, and (2) sub-adult males and sub-adult females using a t-test.

Regression analyses were used to test effects of mean-monthly haul-out abundance, ocean temperature, swell height, and commercial fish landings on social activity of adult male harbor seals from September 1995 to December 1998. I conducted surveys from shore that provided baseline measures regarding relative monthly amounts of near shore, underwater activity of adult males within this community. Counts were conducted during daylight ebb or flood tides while seals were displaced from or gathered near shore. To determine harbor seal abundance, I surveyed haul-out areas during afternoon low tides, when seals prefer to rest ashore. Ocean temperature and swell height measurements were retrieved from NOAA buoy 62042, when operational. When buoy 62042 was ripped away from its mooring by high

seas, ocean temperature and swell height were calculated by interpolating data from a buoy directly north and south of Monterey Bay. I used commercial fish landings supplied by National Marine Fisheries Service (NMFS).

RESULTS

I observed 10 general categories of underwater behavior (Figs. 1 and 2). Nine types of behavior have been described previously: (1) surface splashing [SP], (2) bubble-blowing [BB], (3) vocalizing [VO], (4) paired somersaulting or rolling [RO], (5) mounting [MT], (6) biting [BT], (7) fore-flipper scratching or waving [FS] (8) head-thrusting [HT], and (9) growling [GB]. I defined (10) attending [AT] as approaching and initiating passive muzzle contact with a vocalizing seal. Seals also approached [AP] a vocalizing seal with no subsequent muzzle contact. I also identified two types of rolling [RO]: active [aRO] and passive [pRO]. Active rolling [aRO] occurred when a seal pursued its partner during somersaulting. In contrast, a seal was forced to rotate as a defensive response to pursuit or chase by another seal during passive rolling [pRO].

Underwater behavior occurred throughout all months sampled. Adult males RO and VO throughout fall, winter, and spring (ANOVA; $p < 0.27$ and $p < 0.66$; Fig. 3). Attending [AT] and MT also occurred during each season; however, MT occurred significantly more frequently during spring (1.33) than winter (0.056; Kruskal-Wallis, $p < 0.0033$; Games and Howell method) and AT occurred more frequently during spring (3.0) than fall (0.68, $p < 0.0015$) or winter (0.33, $p < 0.00023$, Tukey's HSD (Spjotvoll/Stoline) test; ANOVA; $p < 0.000014$; Fig. 3).

Frequency of specific types of behavior depended on social class ($X^2 = 1104$, $p < 0.0001$, Table 1, Fig. 4). Adult males VO, SP, and BB significantly more than expected, and pRO, FS and GR less than expected. In contrast, sub-adult males FS, aRO, AT, and MT most frequently, and VO, SP, and BB less than expected. Sub-adult females FS, pRO, and GB significantly more than expected but never VO, SP, or BB (Table 1, Fig. 4). Adult females were never observed engaging in these behaviors other than rebuffing male attention (<1%) or resting (>99%).

Social classes also exhibited differences in RO and AT (Fig. 4). Adult males almost exclusively aRO (>99%). Sub-adult males aRO 91%, and pRO 9% of RO bouts; whereas, sub-adult females pRO more frequently (83%) than aRO (17%). In response to vocalization bouts, adult males AT (86%) more frequently than AP (14%), followed by sub-adult males (73% AT vs. 27% AP). When females responded to calls, they only approached [AP] a vocalizing male, and were never observed attending [AT] or initiating muzzle contact.

Mean duration of rolling bouts between adult males (30.7 sec., SE = 2.8) was significantly greater than rolling bouts between adult and sub-adult males (14.8 sec., SE = 2.3), adult males and sub-adult females (10.0 sec., SE = 1.0), and sub-adults (8.3 sec., SE 0.93; $F = 18.8$, $p < 0.0000001$). Mounting bouts did not differ significantly among social classes ($P = 0.125$). Preliminary results indicated that adult males produced longer duration underwater vocalizations, such as roars, while grunts and growls were more frequently recorded from sub-adult males. These data, however, have not been analyzed to completion.

Two-step sequence analysis of underwater behavior indicated predictable patterns among all social classes (adult males $X^2 = 1577$, $p < 0.0001$; sub-adult males $X^2 = 504$, $p < 0.001$; sub-adult females $X^2 = 80$, $p < 0.01$). Certain types of behavior frequently followed other specific types, but rarely or never others (Fig. 5a, b, and c). For example, adult males frequently VO followed by BB (VO—BB), BB—SP, BT—RO, GB—FS, and FS—HT. Specific types of behavior were often repeated successively, such as SP—SP, VO—VO, RO—RO, and AT—AT (Fig. 5a). Sub-adult males also BB—SP, BT—RO, GB—FS often and repeated a behavior such as SP—SP, RO—RO, AT—AT, and FS—FS (Fig. 5b). Biting—HT and HT—GB were the only significant behavioral sequences of sub-adult females, although these females pRO—FS, FS—GB, and FS-FS most frequently (Fig. 5c).

Using factor analysis of underwater behavior, I generated a model that grouped individual seals by social class (Fig. 6). The model was based upon VO, SP, RO, and FS behaviors. Underwater vocalizing [V0], SP, FS, and RO were related (0.82, 0.70, -0.79, -0.51) to factor 1 scores, and RO and FS related

(-0.84, 0.58) to factor 2 scores. Adult males VO and SP significantly more and FS less than sub-adult males and females ($t = 9.5$, $p < 0.000006$). In addition, sub-adult males RO significantly more and FS less than sub-adult females ($t = 3.0$, $p < 0.04$). I excluded BB, BT, GB, which were significantly correlated with one or more of the behavior used in the model. AP-AT, MT, and HT did not vary markedly among social classes.

Adult male underwater activity was positively correlated with commercial fish landings for California by month ($r = 0.43$, $p < 0.05$; Fig. 7) and year ($r = 0.95$, $p < 0.05$; Fig. 8). In contrast, month, year, mean-monthly ocean temperature, swell height, and harbor seal haul-out abundance were not reliable predictors of near shore activity.

DISCUSSION

Evidence regarding social nature of harbor seals is somewhat controversial. Harbor seals have been described as gregarious ashore but solitary offshore while feeding (Scheffer and Slipp 1944, Bishop 1968), or cohesive and cooperative during foraging (Wilson 1978). Individual associations among seals are either transitory (Knudtson 1974) or represent dominance relationships established during underwater social interactions (Sullivan 1981). During this study, harbor seals exhibited a highly social disposition underwater. Underwater social behaviors included three primary types (1) visual and acoustic displays, such as vocalizing, surface splashing, and bubble-blowing; (2) playful or agonistic social behavior such as rolling, mounting, attending, biting; and (3) signal gestures such as head-thrusting, fore-flipper scratching, and growling (Figs. 1 and 2). These types of behavior have been well-documented in terrestrial mammals (wolf, *Canus lupus*, Mech 1970; lion, *Panthera leo*, Schaller 1972; baboon, *Papio hamadryas*, Abegglen 1984; and chimpanzee, *Pan troglodytes*, Goodall 1986), facilitating maintenance of social organization.

Vocalization displays communicate social status and function primarily to advertise fitness, define territories, or maintain social relationships (red deer, *Cervus elaphus*, Clutton-Brock and Albon 1979; wolf, Harrington and Mech 1979; howler monkey, *Alouatta seniculus*, Sekulic 1982; gibbon sp. *Hylobates*, Cowlishaw 1992). Evidence of this type of communication among harbor seals was males congregating

together during underwater vocalizations and sustaining passive muzzle contact with displaying males [AT] (Fig. 2). An individual is inherently vulnerable to aggression during underwater vocalizations unless socially dominant; therefore, passive muzzle contact from another male may indicate submission (Schenkel 1967, Bekoff 1972). Further evidence regarding the submissive nature of this social behavior includes observations that attending males are generally smaller than displaying males. Attending, therefore, may function to decrease social distance, reduce aggression, and facilitate learning among males.

Fin, tail, or fore-flipper splashing functions primarily as a visual and acoustic display by marine mammals. Marine mammals such as the humpback whale (*Megaptera novaengeliae*), orca (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*), tail and fin splash to signal aggression (Jacobsen 1986, Kaufman and Forestell 1986, Shane 1990). The loud surface percussion, produced by forceful tail or fin contact with ocean surface, may intimidate potential competitors during courtship rituals. Splashing also is common during feeding and play among sub-adults. Bishop (1968) and Wilson (1978) described splashing as solitary play in harbor seals. Harbor seals, however, may also splash during courtship to attract estrous females, intimidate competitors, and assert dominance (Sullivan 1981).

Paired sparring, tumbling, mounting, and biting also may function to assert dominance relationships, decrease social distance, reduce aggression, stimulate learning, and facilitate maintenance of social organization among groups of animals (wolves, Mech 1970; lions, Schaller 1972; macaques, DeVore 1965). Mock fighting is a primary form of social play among Steller sea lion (*Eumetopias jubatus*, Farentinos 1971), elephant seal (*Mirounga*, Bartholomew 1952), and fur seal (*Callorhinus ursinus*, Bartholomew 1959) pups, and sub-adults on the rookeries. This activity presumably facilitates physical and social development. Non-breeding adults engage in more intense, ritualized fighting that never results in injury, but may function to maintain social relationships among individuals on hauling grounds. These interactions all contrast with intense fighting among territorial bulls defending their breeding site (Farentinos 1971). Harbor seals exhibited a similar range in sparring intensity from play to fighting during paired somersaulting, rolling, and biting. Social function, therefore, may include play, social development

or learning, and maintenance of social relationships or dominance hierarchy, depending upon social class of the seals and season of occurrence. All these potential social functions are relevant to community social organization.

Gestures such as fore-limb extension, head-thrusting, and growling may signal solicitation or termination of social encounters. For example, wolves and lions paw, nudge, nip, or nose to initiate play, just as chimpanzees and baboons touch with a hand or gesture with open mouth (Mech 1970, Schaller 1972, Abegglen 1984, Goodall 1986). Similarly, harbor seals used a fore-flipper wave or scratch as a solicitous gesture, or head thrusting and nosing to initiate wrestling and rolling with other seals. Seals also used gestures to terminate social interactions. Growling with an expulsion of bubbles was used as an acoustic and visual gesture to prevent social contact or signal defensive posture in response to another seal's aggression. Seals combined this defensive signal with fore-flipper waving or a head-thrust, then sank in the water column or fled to avoid further social contact.

Evidence that adult males were socially active throughout the year, displaying underwater (VO) and sparring (RO) equally among seasons (Fig. 3), and exhibiting complex social behavior such as attending [AT] (Fig. 2 and 3), corroborated previous conclusions regarding the role of aquatic behavior in establishing and maintaining social hierarchy (Sullivan 1981). Increased attending and mounting during spring may indicate an intensification of these social relationships before mating season when males experience extreme competition for breeding privileges. To further investigate development of behavior and its role in social organization, I included observations regarding the social nature of sub-adult males and females.

Underwater observations of adult males, sub-adult males, and females indicated that social behavior may reflect differences in social status. In studies of harbor seal social behavior ashore, adult males were dominant to sub-adult males, and sub-adult females were submissive to all other social classes (Sullivan 1982). This pattern is also evident among these harbor seals offshore. For example, adult males primarily performed acoustic and visual displays such as roaring, splashing, and bubble blowing (Fig. 4),

which ultimately function to advertise their presence and draw attention from other seals. These types of behavior generally indicate social dominance, and the social repercussions or risk of retaliation from a higher ranking male is relatively insignificant. In contrast, sub-adult males performed fewer displays, instead exhibiting submissive or playful social behavior such as attending, mounting, flipper scratching, and rolling. Sub-adult females were socially submissive, and primary recipients of aggression from other social classes; therefore, exhibited the least aggressive gesture, fore-flipper scratching (FS); the most defensive response to social encounter, bubble-growling (GB); and the greatest incidence of passive rolling (pRO; Fig. 4).

Differences in underwater behavior also may relate to varying selective pressures associated with each social class. For example, adult females require resources to exclusively raise young, therefore, they primarily rest between foraging trips to conserve energy and build fat stores necessary to nurse pups. In contrast, males, free from parental responsibility, increase reproductive fitness by acquiring as many mates as possible, therefore, exclusively performing acoustic and visual displays that function as advertisement or competition among males for breeding privileges with estrous females. Free from the energetic burden of reproduction, sub-adult males may have more leisure time and a greater tendency to participate in playful social behaviors (Fig. 4)

Specific kinds of behavior exhibited also may be related to developmental differences between adult and sub-adults. For example, underwater vocalizations, such as roars, may require mature vocal tracts or folds, a minimum level of hormone testosterone, and experience. This may explain why underwater roars were performed only by adult males. Sub-adult males performed underwater vocalization displays infrequently, using only grunts and growls, but spent more time attending and rolling with other males presumably because these behaviors provide a social context for play and learning. These social experiences are necessary to mature developmentally and socially, and eventually compete among adults. With regard to differences in behavior between adult and sub-adult females, immature females have never mated, therefore, do not have the energy constraints of pregnant adults but require social experience

necessary to assess potential mates by approaching calls of males, rolling, mounting, teasing, or flipper scratching attentive males. These kinds of behavior may function to facilitate social acuity or maturity without risking physical harm or aggression from males.

Two step sequence analysis is a relatively simple way of beginning to understand how types of underwater behavior relate to one another. Identifying these relationships may provide insights regarding social function. For example, specific behavior that frequently follows other types of behavior in sequence presumably indicates similar social context. Male harbor seals VO, SP, and BB frequently in sequence, which is consistent with their function as acoustic and visual displays. Similarly, HT, BT, RO, MT, and FS occurred together in sequence during paired agonistic or playful sparring between males. Finally, attending was related primarily to passive FS and MT, and never followed by aggressive displays, such as RU, SP, or BB. This is consistent with the hypothesis that attending may indicate subordinate social rank (Fig. 5a).

These general patterns also were evident among sub-adult males. A notable exception, however, was that FS frequently followed other specific types of behavior such as RO, MT, AT, BT, and GB, indicating that sub-adult males may have been frequently outmatched during competitive or playful interactions and responded with a gesture to terminate social contact (Fig. 5b). Similarly, females exhibited this FS gesture in response to every other behavior (AP, RO, MT, BT, HT, and GB), possibly as a result of their vulnerability to aggression or harm during social interactions with seals of greater social status (Fig. 5c). These significant patterns indicated that social behavior of these harbor seals was predictable, representing logical sequences reflecting social disposition or status, functioning to facilitate maintenance of social organization, and reduce aggression among individuals within the herd.

The model derived from factor analysis is an extension and simplification of my results regarding behavioral differences among social classes, and indicated that social class could be predicted from four primary underwater types of behavior: vocalizing [VO], splashing [SP], rolling [RO], and flipper-scratching [FS]. Individuals within each social class exhibited a characteristic repertoire of behavior regardless of social context (Fig. 6). Social classes performed underwater behavior such as AT-AP, MT

and HT more or less equally; however, closer examination of social context may indicate differences that reflect dominance relationships or social status among individuals.

The central California coast is a region of upwelling characterized by high primary productivity. This productive environment supports a rich food supply for marine mammals and consequently may influence social nature of harbor seals. Social activity of male harbor seals was significantly correlated with fish landings for California, indicating that social nature of harbor seals may be dependent on ease of securing adequate food resources (Figs. 7 and 8). Yearly comparison of fish landings or potential food resources with social activity was a more reliable indication of this relationship ($r^2 = 0.90$; Fig. 8) than monthly comparison ($r^2 = 0.16$; Fig. 7c) presumably because fish landing are not always assigned to the appropriate month when they occur (Leos, CDFG, pers. comm.), and response of harbor seal activity to food supply may not be immediate but delayed in time and dependent on the health and condition of the animals.

During this three-year study, squid and anchovy stocks fluctuated from record highs to relative scarcity coincident with strong upwelling signals followed by a prolonged and intense El Nino (CDFG). When abundant, these schools occur within a few hundred meters of sites where harbor seals rest ashore. Although harbor seals in California feed primarily on widely distributed demersal fishes (Harvey and others, 1995), seasonally abundant schooling fishes and cephalopods may represent a resource boon during which seals have an energy surplus or more leisure time. From a physiological perspective, Barber (1991) suggested under these conditions, sub-adults and adults may increase social activity, such as play, because of benefits accrued during physical activity including increased resistance to pathogens and hypothermia. This increase in social activity may create a need among these harbor seals for social behavior that functions to decrease social distance, reduce aggression, and facilitate maintenance of social organization.

Harbor seals require essential resources such as food and mates to survive and reproduce. Competition for food and mates varies from season to season and year to year depending on resource distribution and availability. For example, female harbor seals are only receptive for mating during a day

or two in spring near the end of their lactation; therefore, competition among males for access to estrous females may be intense but brief. In addition, these harbor seals live along a relatively productive coastline with seasonal oceanographic upwelling that supplies nutrients necessary to sustain a rich and diverse stock of potential prey. During years with strong upwelling pulses, these seals may experience more leisure time and energy to socialize throughout the year than seals living under more temporally or geographically stressful environmental regimes. For example, fish species abundance and diversity along the California coast is significantly greater than in Scotland's Moray Firth. Coincidentally, harbor seals in the Moray Firth only perform underwater vocalization displays during mating season (Van Parijs and others, 1997), and information regarding their year-round social behavior is scarce. Similarly, seals in Monterey during an El Nino event exhibited reduced social activity (Figs. 7 and 8).

During oceanographically productive years, however, seals along Monterey coast exhibited social behavior underwater throughout the year, indicating use or need of social rituals which reduce aggression and facilitate social bonds among members of the herd. Gregarious behavior, such as attending among males during underwater vocalization displays, peaked before mating season and may allow males to sort out social relationships, assess competition, and acquire effective individual strategies for attracting females during mating season based on social status. Social interactions among males and females observed before breeding season may also facilitate mate selection during breeding season. In the following chapter, underwater behavior and social interactions among individual males were examined to better understand the function of underwater vocalization displays regarding social and mating strategy.

Table 1. Contingency table comparing actual and (expected) frequency of underwater behavior (vocalizing [VO], flipper-splashing [SP], bubble-blowing [BB], attending [AT] or maintaining passive muzzle contact with vocalizing males, approaching vocalizing males [AP], active paired-somersaulting or rolling [aRO], passive rolling [pRO], mounting [MT], biting [BT], fore-flipper scratching or waving [FS], head-thrusting [HT], and growling [GB]) among social classes (adult males [AM], sub-adult males [SM], sub-adult females [SF]). Bold numbers with asterisks indicate behavior observed significantly more frequently than expected. Italicized numbers with asterisk indicate behavior observed significantly less frequently than expected.

	VO	SP	BB	AT	AP	aRO	pRO	MT	BT	FS	HT	GB
AM	**353*** (**217**)	**197*** (**132**)	**121*** (**78**)	70 (60)	11 (19)	143 (124)	*1** *(34)*	*12** *(36)*	42 (40)	*33** *(206)*	40 (51)	*10** *(37)*
SM	*7** *(65)*	*22** *(39)*	*9** *(23)*	**29*** (**18**)	11 (6)	**54*** (**37**)	10 (10)	**25*** (**11**)	17 (12)	**90*** (**61**)	19 (15)	15 (11)
SF	*0** *(79)*	*0** *(48)*	*0** *(28)*	*0** *(22)*	9 (7)	*9** *(45)*	**45*** (**12**)	22 (13)	7 (14)	**219*** (**75**)	26 (19)	**37*** (**14**)

Figure 1. Underwater images of harbor seal behavior: (a) vocalizing [VO], (b) paired-somersaulting or rolling [RO], (c, f) mounting [MT], (d) surface-splashing [SP], and (e) bubble-blowing [BB].

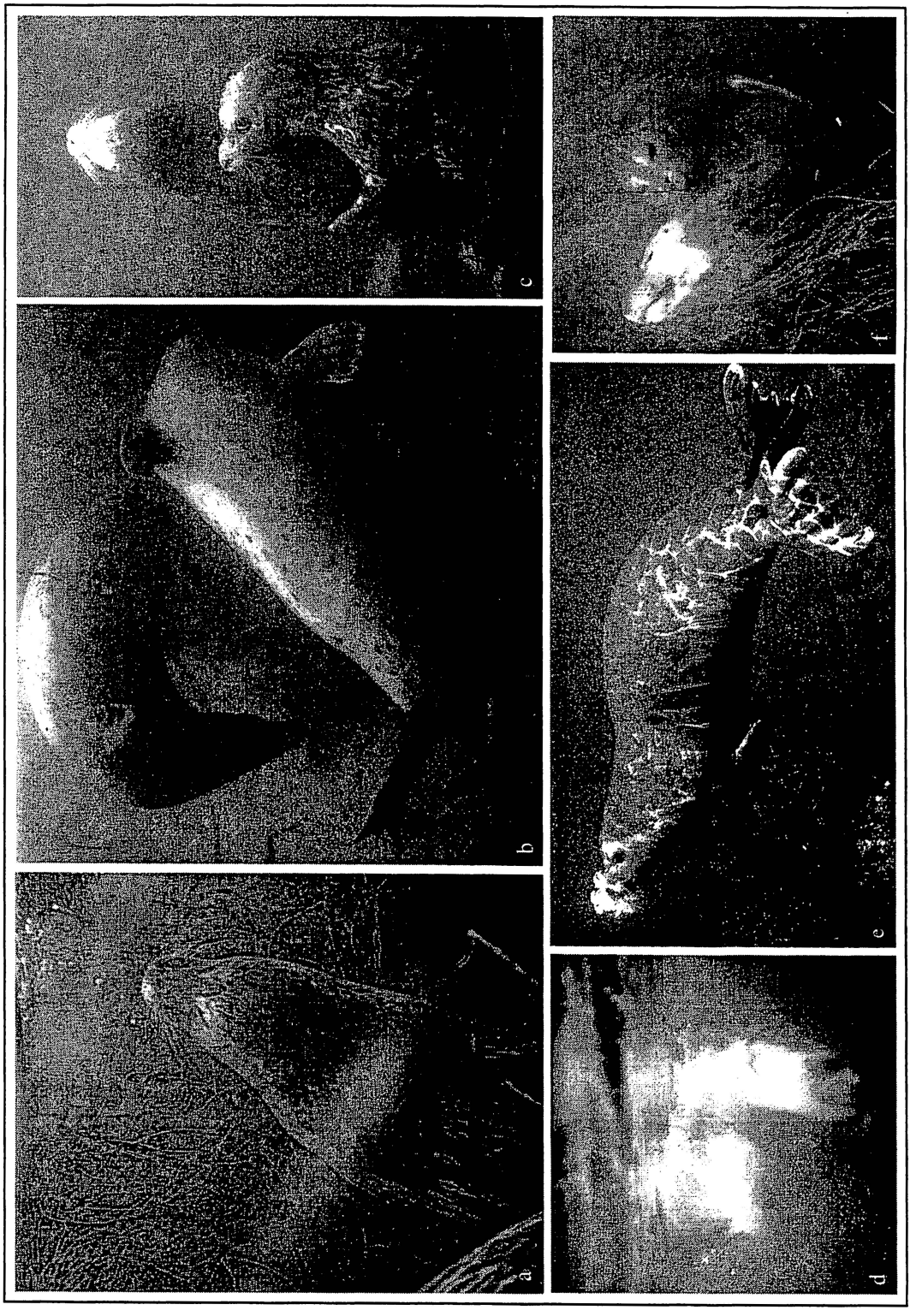

a
b
c
d
e
f

Figure 2. Underwater images of behavior: (a,b) maintaining passive muzzle contact or attending [AT] a vocalizing male, indicated by arrow, (c) rolling [RO] while flipper and tail biting [BT], (d) neck-biting [BT], and (e) fore-flipper scratching [FS].

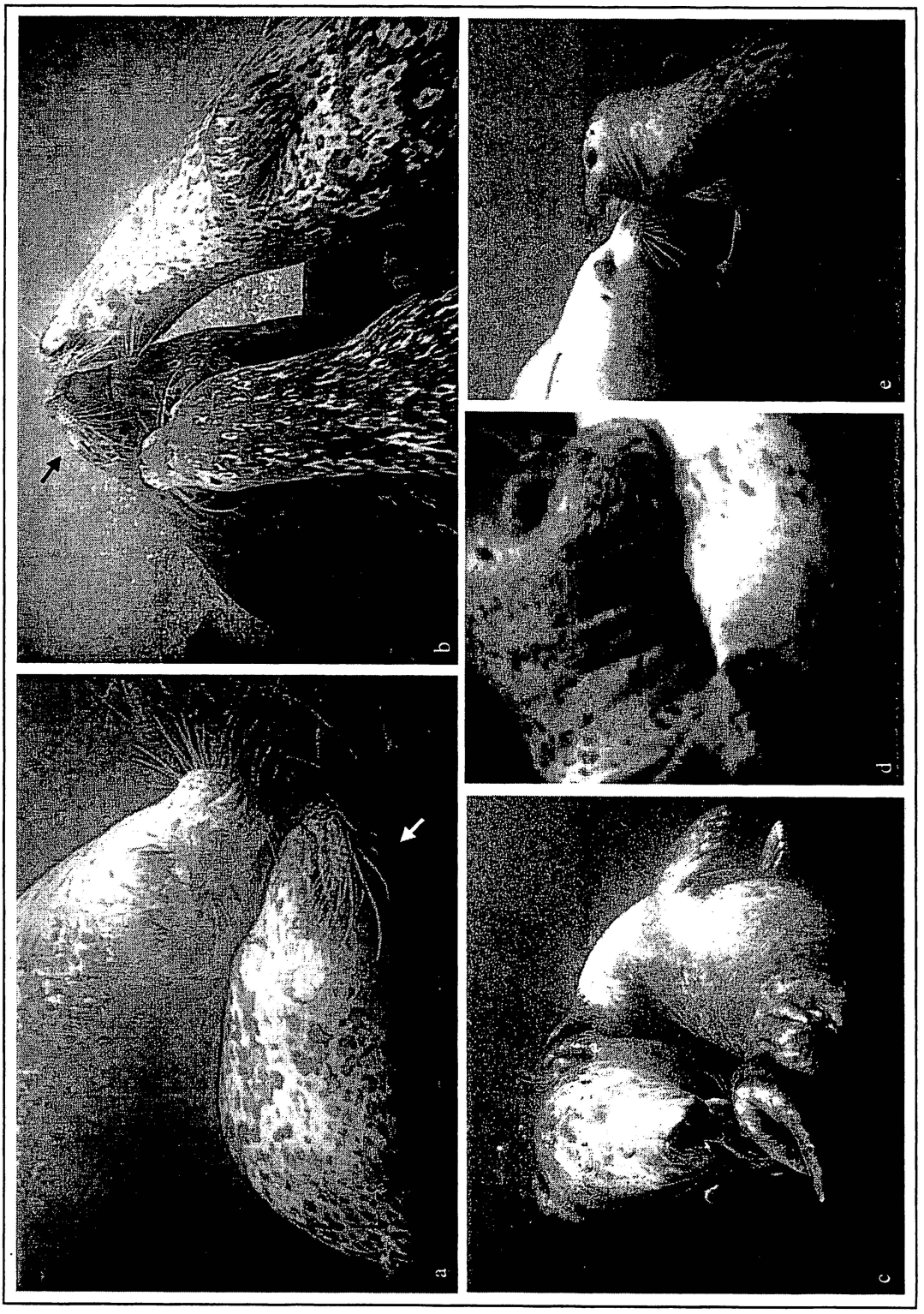

a
b
c
d
e

Figure 3. Daily mean abundance (± SE boxes, min. and max. vertical lines) of adult males observed performing underwater behavior during surveys from September 1996 to May 1997.

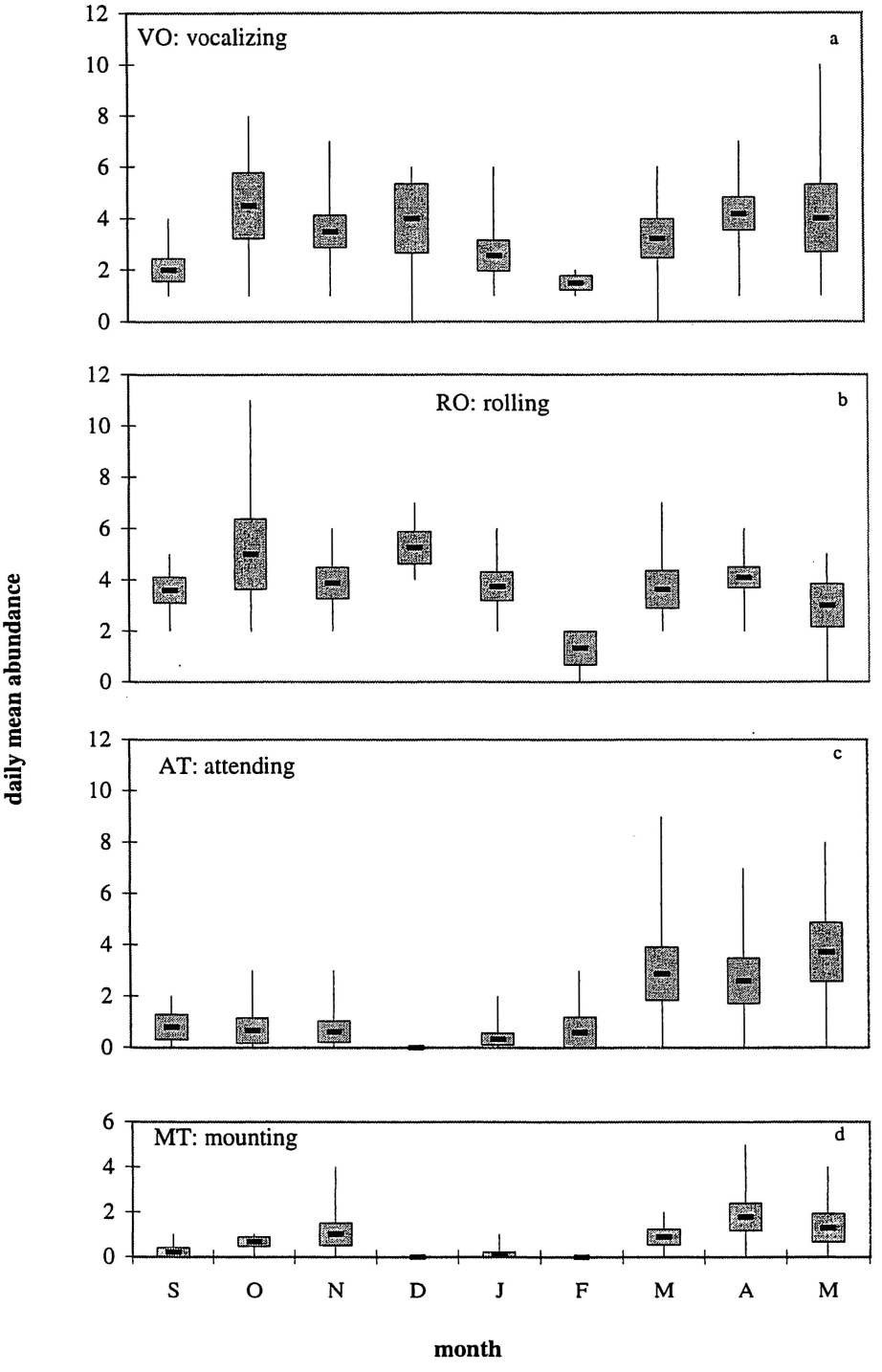

VO: vocalizing
a
RO: rolling
b
AT: attending
c
MT: mounting
d
daily mean abundance
S
O
N
D
J
F
M
A
M
month

Figure 4. Relative frequency of behavior types (VO = vocalizing, SP = splashing or flipper slapping, BB = bubble blowing , AT = attending, AP = approaching a vocalizing male, aRO = active rolling, pRO = passive rolling, MT = mounting, BT = biting, FS = flipper scratching or waving, HT = head thrusting, and GB = growling) among adult males, sub-adult males, and sub-adult females.

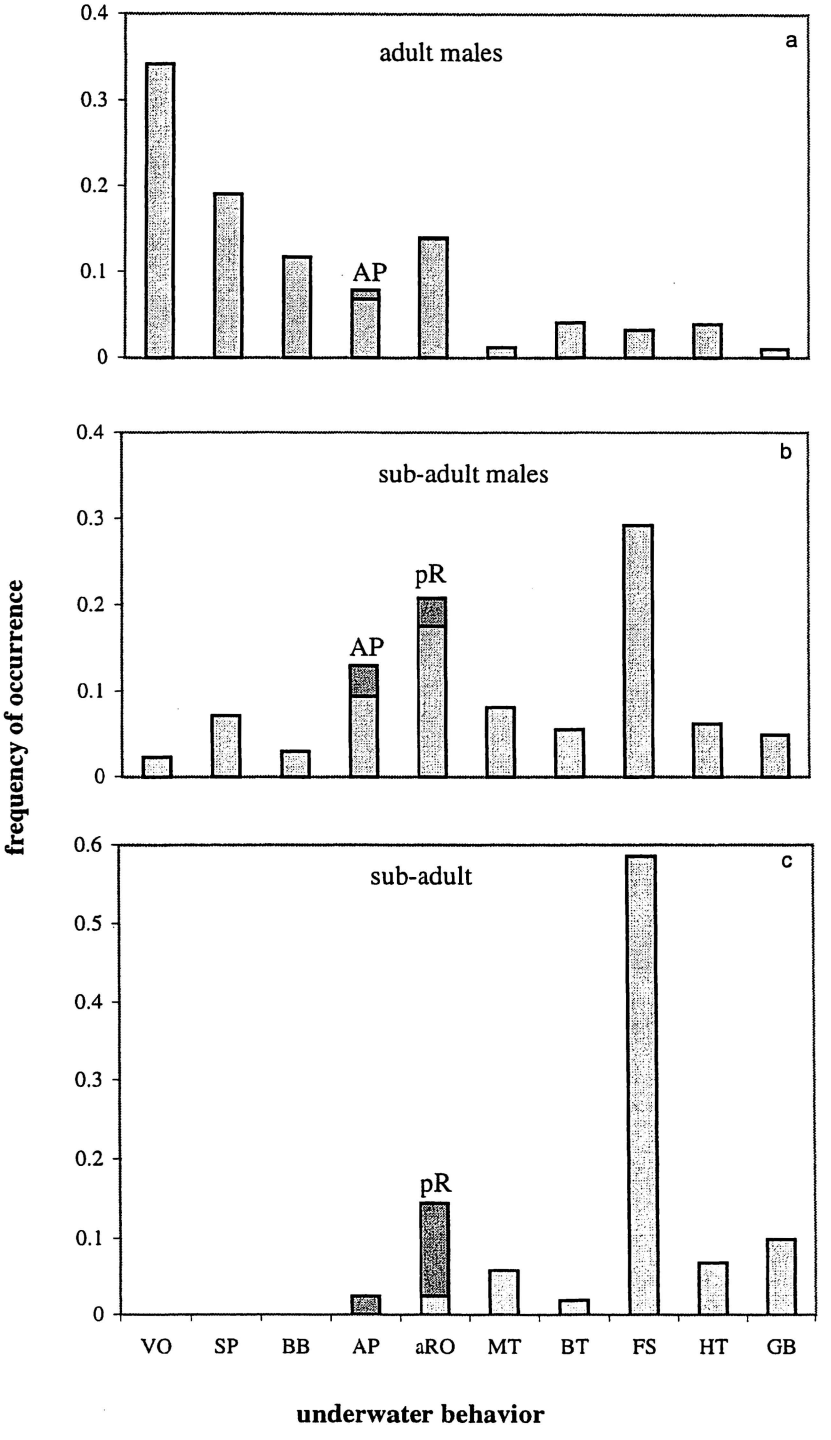
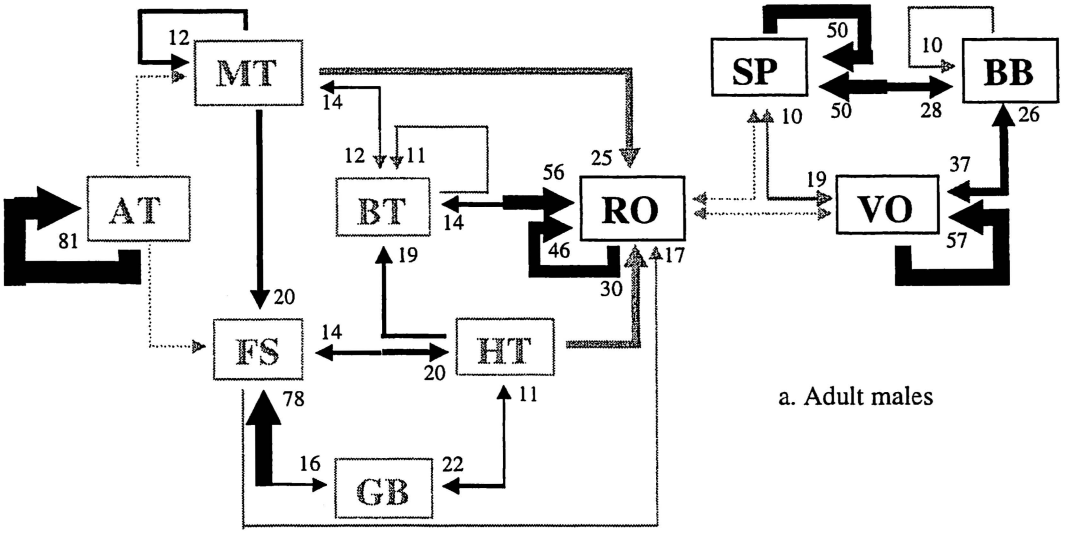
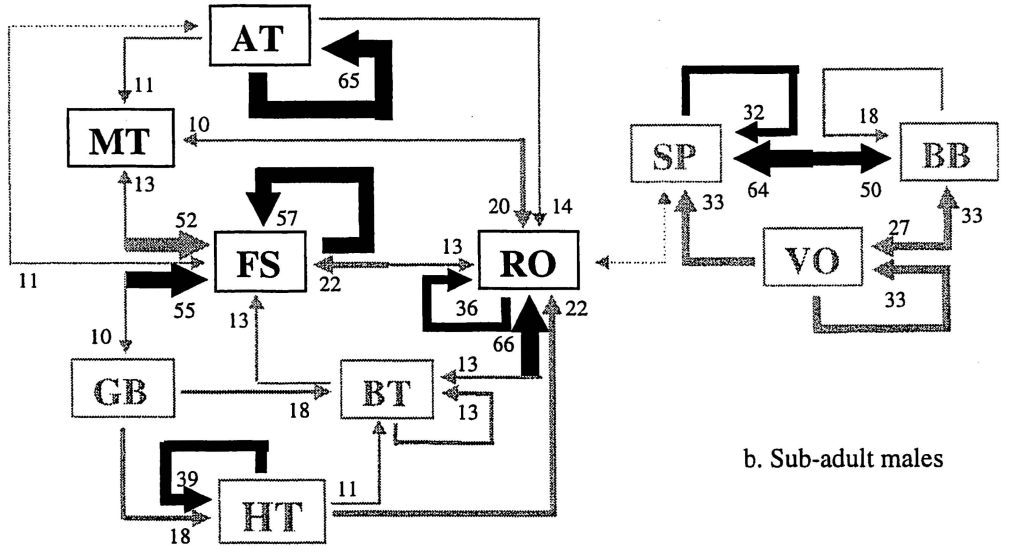

adult males
a
sub-adult males
b
sub-adult
c
AP
pR
frequency of occurrence
underwater behavior
VO
SP
BB
AP
aRO
MT
BT
FS
HT
GB

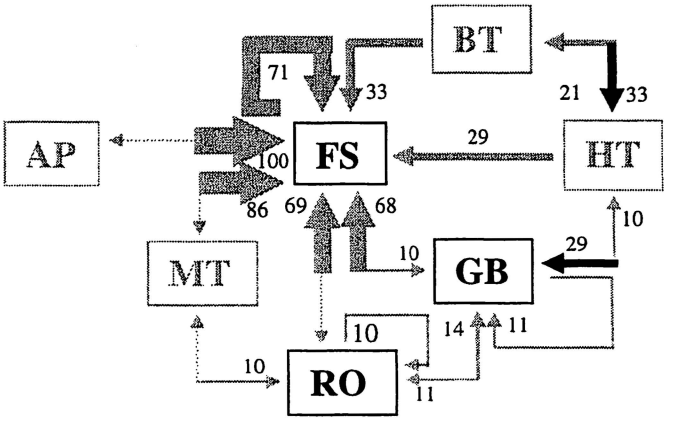
Figure 5. Adult male (a), sub-adult male (b), and sub-adult female (c) two-step behavior (VO,SP,BB,AT,RO,MT,BT,FS,HT,GB) sequences. Arrow point and thickness indicate direction and strength of sequence relationship between types of behavior. Black arrows mark statistically significant sequences based on X^2 contingency table analysis. Numbers indicate percent frequency one behavior followed another. Unlabeled, dotted arrows represent sequences with frequency less than 10%, included only when no greater frequency connections leading to or from a behavior were evident. Black highlighted behavior boxes indicate types of behavior with frequency greater than 10%.



a. Adult males



b. Sub-adult males



c. Sub-adult females

Figure 6. Factor scores of adult males (individuals AM1, AM2, AM3, AM4, AM5, AM6, AM7, AM8, AM9), sub-adult males (SM1, SM2, SM3), and sub-adult females (SF1, SF2, SF3) based on underwater behavior (VO, SP, RO, FS). Discrete groupings AM, SM, and SF (circled) indicated each social class exhibited a characteristic repertoire of underwater behaviors.

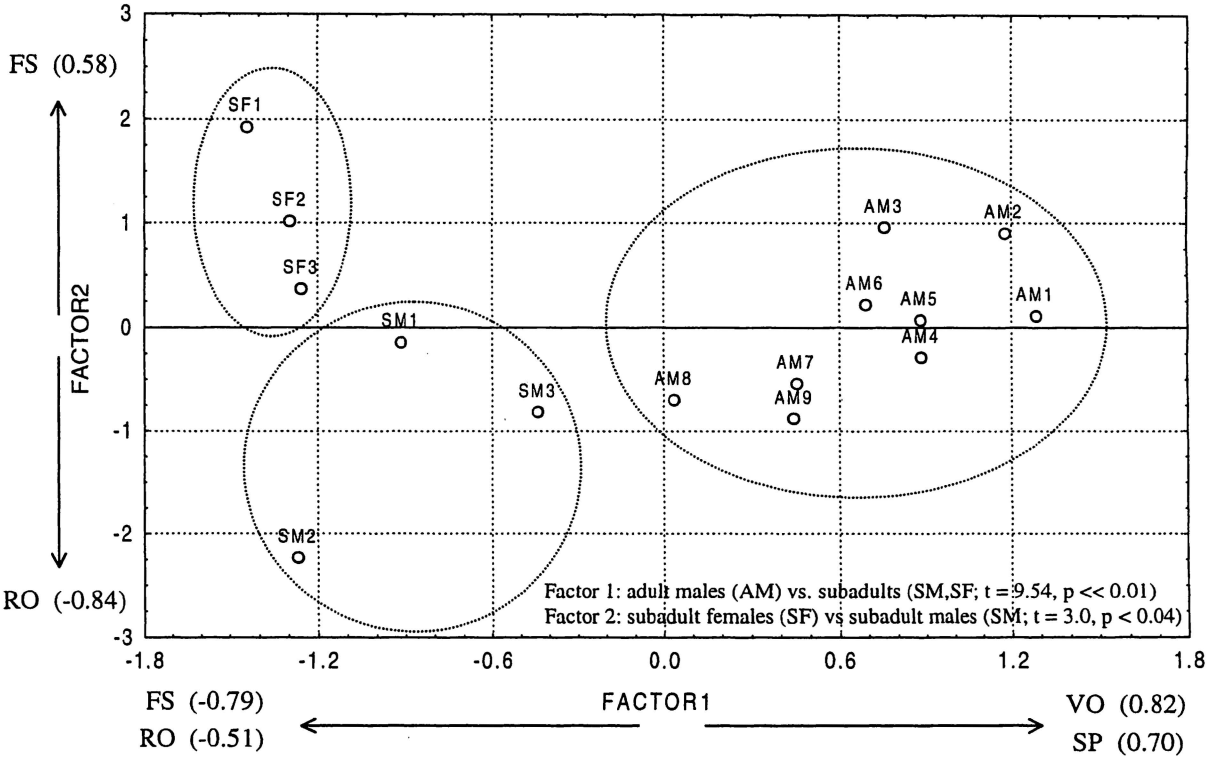

FS (0.58)
RO (-0.84)
FACTOR2
FACTOR1
FS (-0.79)
RO (-0.51)
VO (0.82)
SP (0.70)
SF1
SF2
SF3
SM1
SM2
SM3
AM1
AM2
AM3
AM4
AM5
AM6
AM7
AM8
AM9
Factor 1: adult males (AM) vs. subadults (SM,SF; t = 9.54, p << 0.01)
Factor 2: subadult females (SF) vs subadult males (SM; t = 3.0, p < 0.04)

Figure 7. Mean daily abundance (± SE boxes, min., and max.) of adult males performing underwater behaviors (a) during months from September 1995 to May 1998 correlated (c) significantly with monthly CA fish landings (b; $r = 0.43$, $p < 0.05$).

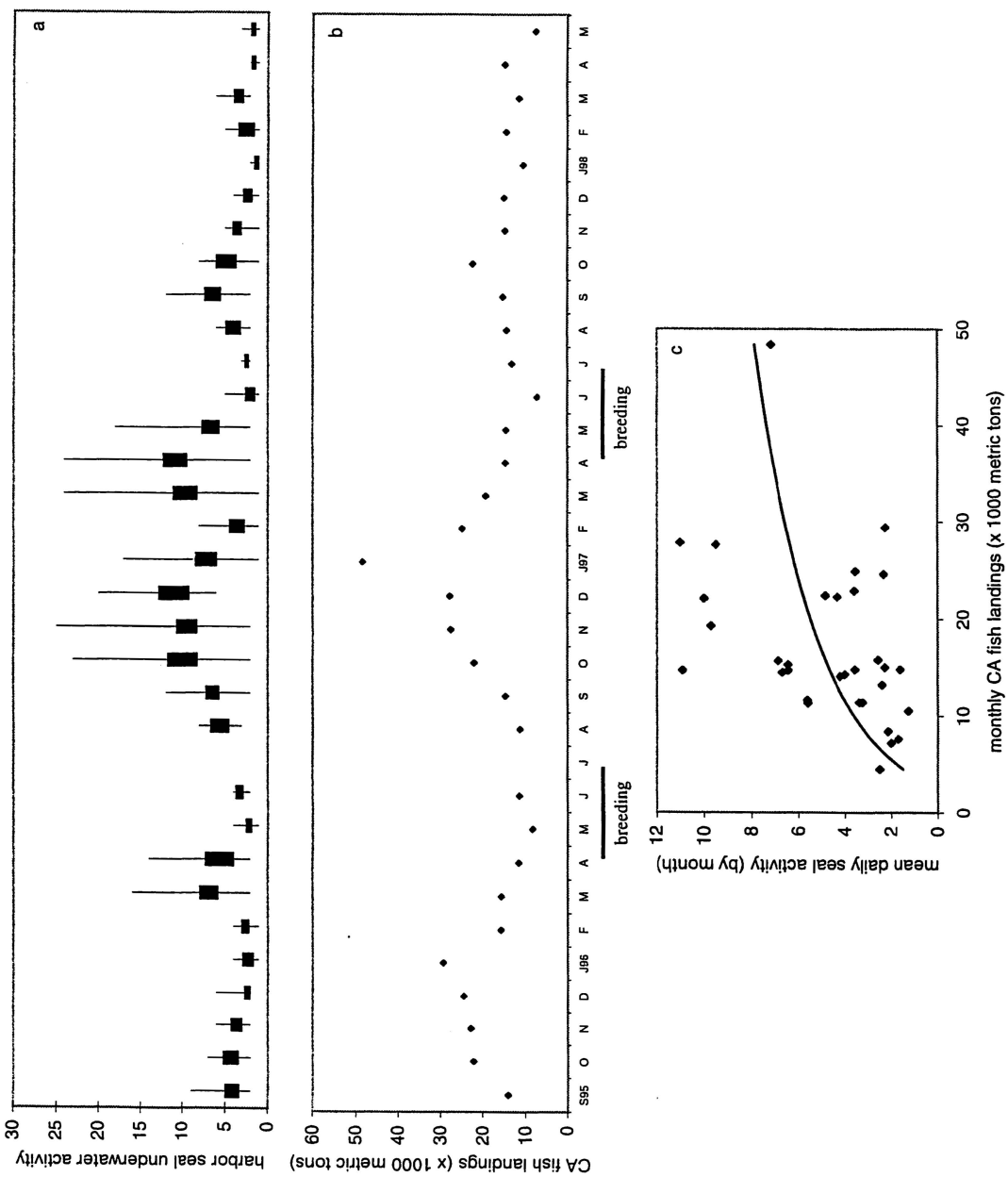
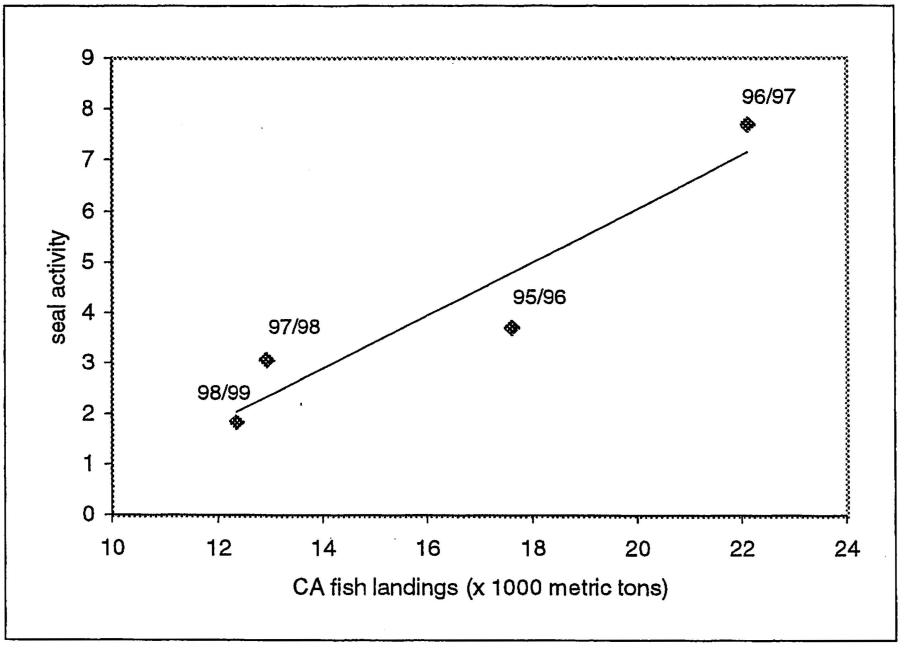

a
harbor seal underwater activity
30
25
20
15
10
5
0
b
CA fish landings (x 1000 metric tons)
60
50
40
30
20
10
0
breeding
breeding
S95 O N D J96 F M A M J J A S O N D J97 F M A M J J A S O N D J98 F M A M
c
mean daily seal activity (by month)
12
10
8
6
4
2
0
0 10 20 30 40 50
monthly CA fish landings (x 1000 metric tons)

Figure 8. Mean daily abundance of adult males performing underwater behavior during observation years 1995/96, 1996/97, 1997/98, and 1998/99 (September through May) correlated significantly with total CA fish landings ($r = 0.95$, $p < 0.05$). Year 1998/99, however, only represents fall months in 1998, because CA fish landings for 1999 have not yet been published.


9
8
7
6
5
4
3
2
1
0
seal activity
96/97
95/96
97/98
98/99
10
12
14
16
18
20
22
24
CA fish landings (x 1000 metric tons)

CHAPTER 3:

UNDERWATER VOCALIZATIONS, BEHAVIOR, AND SOCIAL HIERARCHY AMONG ADULT MALES

INTRODUCTION

The harbor seal (*Phoca vitulina richardsi*) mating system is polygynous (Bartholomew 1970, Le Boeuf 1991). Polygynous mating systems are characterized by variability in reproductive success that depends upon establishment of dominance relationships among males competing for access to estrous females. In reproductive systems of pinnipeds that mate on shore, such as otariids, elephant seal (*Mirounga angustirostris* and *Mirounga leonina*), and grey seal (*Haliochoerus grypus*), dominance relationships are established by resource or female defense strategies (Bartholomew 1970, Boness 1991, Le Boeuf 1991). Dominant males obtain breeding privileges by controlling access to terrestrial breeding habitat required by females. Harbor seals, in contrast, mate offshore where males are unable to compete for these resources. Alternative mating strategies for harbor seals include establishment of leks, dominance hierarchies, or underwater territories (Sullivan 1981, Le Boeuf 1991, Hanggi and Schusterman 1994, Thompson and others 1994, Van Parijs and others 1996).

During the breeding season, male harbor seals may maintain leks, dominance hierarchies, or underwater territories by performing underwater acoustic displays (Hanggi and Schusterman 1994, Coltman and others 1996, Van Parijs and others 1997). Similar hypotheses regarding the function of vocalizations in mating strategy have been described for other pinnipeds that mate underwater, such as the bearded seal (*Erignathus barbatus*; Ray and others 1969, Cleator and others 1989, Ajmi 1996), harp seal (*Pagophilus groenlandicus*; Mohl and others 1975), leopard seal (*Hydrurga leptonyx*; Rogers and others 1996), ringed seal (*Phoca hispida*; Stirling 1973, Kunnasranta and others 1996), and walrus (*Odobenus rosmarus*; Ray and Watkins 1975, Stirling and others 1987). How females choose a mate, however, is poorly understood because reproductive behavior has not been observed directly.

Male harbor seals may communicate their fitness to females during underwater vocalizations by exhibiting differences in sound frequency characteristics (Hanggi and Schusterman 1994). These characteristics may correspond with a male's physical attributes, such as size or health, which are relevant to mate selection either as (1) a direct advertisement to females or (2) signal to competing males regarding fighting ability or

social status. Determination of social function of these male underwater vocalizations with respect to mating and social strategies, however, requires an understanding of their underwater social behavior.

The aim of this study was to investigate social function of underwater vocalization displays. I present evidence that males use these calls to establish and maintain dominance relationships, and social status may correspond with vocalization characteristics such as duration and frequency (Hz). These hypotheses are based on observations that male harbor seals perform underwater vocalization displays and social behavior year-round. Specifically, males congregate during underwater displays by approaching and 'attending,' or establishing passive muzzle contact with a vocalizing male (Fig. 1). Attending seals are presumably subordinate in social status (Nicholson, unpubl. data), generally smaller than the vocalizing male, and exhibit no aggression during this social interaction.

During this study, social function of underwater vocalizations was investigated by examining vocalization and social behavior of individual males. Specifically, I (1) provide a preliminary description of vocalization characteristics of individuals within a harbor seal community with an emphasis on determining acoustic parameters for comparing differences reliably among individuals, (2) correlate differences in acoustic characteristics with observed social behavior during and subsequent to underwater vocalizations by determining how vocalization characteristics of adult males routinely attended during acoustic displays differ from lone vocalizing males, (3) determine whether males exhibit other social behaviors that may indicate social status, (4) generate a model social hierarchy based on social interactions among these males, and (5) compare social status of adult males with their vocalization characteristics.

I predicted that males would exhibit differences in vocalization characteristics such as duration and frequency (Hz). Seals may assess fighting ability or social rank based on these acoustic cues, and respond by ignoring, attending, or sparring depending upon their own social rank or risk of injury during a confrontation. Males with longer, deeper vocalizations should be attended more frequently than other males, and exhibit other aggressive social behavior or displays, such as flipper splashing, which may intimidate potential competitors. Social interactions among individual males should indicate a social hierarchy, which may be relevant to their

overall reproductive success. Social rank of individuals may be reliably predicted from acoustic cues such as roar duration or sound frequency.

METHODS

Underwater vocalizations of individually identified adult males were obtained from twenty (20) hours of Hi-8 video/audio tapes recorded from November 1996 to May 1997 off Pacific Grove, CA, using a housed Sony TR81 video camera and hydrophone. Individuals were recognized by unique pelage patterns. I generated spectrograms of each vocalization using the sound analysis program Canary (frame size 512 samples 50% overlap, Hamming window, filter bandwidth 175 Hz). Sampling rate was 22.05 kHz. Analyses were limited to eleven males from which I was able to record a minimum of ten (10) vocalizations.

Underwater vocalizations were divided into three parts: preroar, step, and roar (Fig. 2). Grunts, groans and creaks (Hanggi and Schusterman 1994) also were recorded, but not frequently enough for analysis. I measured the duration of preroar, step, and roar for each vocalization, and sound frequency of roars by calculating the mean first formant frequency (F_o) or lowest energy band of the vocalization. Mean roar frequency (F_o) of the most frequently observed seal recorded in opposite orientations—facing towards and away from the hydrophone—but at constant depth and distance, was compared using a Student's *t* test to determine the reliability of this frequency measure.

I categorized vocalizations of the most frequently recorded adult male by his orientation to the hydrophone at constant depth and distance to determine effects of orientation on sound propagation or sound spectral characteristics recorded by the hydrophone, and investigate the reliability of spectral measurements. Two orientation categories were defined as (1) the seal facing away from the hydrophone by more than 120 degrees or (2) toward the hydrophone by less than 60 degrees. Spectral characteristics were compared by computing the cross-correlation between each pair of spectra (Zar 1996). To determine whether orientation affected spectral characteristics, I used a Student's *t* test comparing mean cross-correlation of roars recorded from (1) similar orientation—roars facing the hydrophone compared with other roars facing the hydrophone, or

roars facing away from the hydrophone compared with other roars facing away—and (2) opposite orientation—roars facing the hydrophone compared with roars facing away.

Individual adult males were classified into two distinct behavior categories: attended and lone roaring seals. Attended males (n = 3) attracted nearby males that sustained passive muzzle contact with the vocalizing seal during more than 85% of underwater vocalization bouts. Lone roaring males (n = 6) vocalized alone during more than 95% of vocalization bouts. I compared mean duration of call types (preroar, step, and roar), and sound frequency (F_o) of roars between attended and lone seals using a Student's *t* test. Mean frequency (F_o) of roars was compared among all individuals using a single factor non-parametric ANOVA (Kruskal-Wallis test) and Games and Howell multiple comparison tests. Two males, attended during 35% and 22% of vocalization bouts, fit criterion for neither 'attended' nor 'lone' roaring males, therefore, were excluded from this analysis.

Social behavior of seventeen (17) individual males was categorized into four primary types: underwater vocalization displays or roaring (RU), paired somersaulting or rolling (RO), approaching and initiating passive muzzle contact with a vocalizing male (AT), and fore- or hind-flipper surface splashing (SP). I further subdivided (SP) into group-splashing (SPg) and solo-splashing (SPs) to specify whether the behavior was directed toward other seals (SPg), or performed alone (SPs). The frequency each male was attended during underwater vocalization displays also was calculated. I then compared relative frequency of behavior for each male using factor analysis, and performed a t-test to compare factor values of frequently attended (>20% of vocalization bouts) and lone roaring males to determine differences in behavior between these two groups.

I compared underwater social behavior and roar characteristics among eleven individual males using canonical analyses. Social behavior was categorized into five primary types: roaring while other males maintained passive muzzle contact (RW), lone roaring (RA), RO, AT, SPg, and SPs. Roar characteristics included duration (s) and sound frequency (Hz). I performed correlation analysis among all types of behavior. Significantly correlated types of behavior were excluded from canonical analysis.

I recorded aggressive and submissive social interactions among 23 individual adult males. Aggressive behavior included charging, lunging, chasing, or splashing another seal. Cowering or fleeing represented submissive behavior. Other agonistic categories of behavior were related specifically to underwater vocalization displays. For example, I defined attending as submissive. In contrast, directed and intentional interruption or disturbance of vocalization displays was scored as aggressive. Using this information I constructed a matrix representing all possible pairings among males. Pairings were scored as wins (+1), losses (-1), or ties (0). I used skew-symmetry analysis following Gower (1987) to derive a theoretical hierarchy among individual males based on their social interactions. Correlation analysis was performed between social rank derived from skew-symmetry analysis and (1) roar duration, and (2) roar frequency (Hz).

RESULTS

Preroar was the lowest and narrowest frequency (<250 Hz) vocalization, and preceded steps and roars in call sequence (Fig. 2). Mean duration of preroar was 1.9 s ± 0.15 SE, ranging from 0 to 7.9 s. Roars were non-harmonic, flat-spectrum calls with primary frequency ranging from 50 to 3000 Hz, broad frequency bands resembling formants, and mean duration of 2.4 s ± 0.25 SE. Steps resembled roars with frequency range less than 1000 Hz. This call was the shortest of the three types with a mean duration of 0.88 s ± 0.20 SE.

Orientation of a seal with respect to the hydrophone significantly affected sound spectra of underwater roars. Specifically, peak frequencies between 50 and 3000 Hz and intensity levels (dB) of roars were more positively correlated when seals were recorded from a similar orientation, either facing towards or away from the hydrophone ($r = 0.47 \pm 0.04$ SE), than an opposite orientation, facing towards and away from the hydrophone ($r = 0.29 \pm 0.04$ SE, $t = 3.0$, $p = 0.01$, $n = 55$). Mean first formant frequency, however, was not significantly affected by orientation, or whether a seal faced towards (184.6 ± 5.0 SE) or away (178.8 ± 7.4 SE) from the hydrophone while vocalizing (F_o, $t = 0.88$, $p = 0.40$, $n = 11$).

Attended males spent significantly more time (20%) roaring while vocalizing than lone males. Lone males spent 6% more time preroaring, and 22% more time step calling than attended seals (Table 1). Mean roar duration of attended seals was 1.3 s greater, and mean roar frequency (F_o) was 39 Hz less than lone seals;

therefore, attended seals produced longer, deeper roars than lone-roaring seals (Table 1). These differences in roar characteristics between the two groups are apparent when mean frequency (F_o) and duration are plotted together (Fig. 3). Two seals, males 5 and 6, attended during 35% and 22% of vocalization bouts, respectively, also were included. Roar characteristics for these two individuals fell in a range between attended and lone roaring seals. Mean frequency (F_o) among the original nine seals (1,2,3,12,14,18,19,22) also was significantly different (Kruskal-Wallis, $X^2 = 84.0$, $p << 0.01$), but only for seven of 36 paired comparisons, or seals with frequency differences greater than 30 Hz.

Using factor analysis to compare social behaviors between attended and lone roaring males, Factor 1 was positively correlated with RO (0.64) and AT(0.51), and negatively correlated with RU (-0.83) and SPg (-0.62; Fig. 4). Attended males, therefore, roared [RU] and group splashed [SPg] more than lone-roaring males, whereas lone-roaring males rolled [RO] and attended [AT] more frequently ($t = 6.9$, $p << 0.01$). Solo splashing [SPs] was negatively correlated with roaring (-0.63); therefore, seals who roared frequently spent less time splash displaying while alone than seals who roared infrequently.

Using canonical analyses, social behaviors and roar characteristics were significantly correlated (canonical $r = 0.98$, $X^2 = 26.9$, $p = 0.00015$, Fig. 5). Vocalization characteristics were most significantly correlated with RW (0.98) and SPg (0.53). Roar length was a more reliable indicator (0.87) of these behaviors than roar frequency or pitch (0.70). Overall, seals with longer, deeper roars spent more time attended roaring [RW] and splash displaying in social groups [SPg] than seals with shorter, higher pitched roars. Roaring alone [RA], rolling [RO], and splashing alone [SPs] were negatively correlated (-0.87), (-0.70), and (-0.66) with RW, respectively; therefore, seals frequently attended during roaring spent less time lone roaring, lone splashing, or rolling with others than seals who were infrequently attended.

Analysis of asymmetrical social interactions between pairs of individual males indicated a social hierarchy (Fig. 6). The social hierarchy was pyramidal or characterized by horizontal spreading from the center origin, indicating deviations from a linear hierarchy. Social relationships among seals, therefore, were not always clearly defined. Several social relationships, however, were obvious. For example, seal 1 and seal 2

dominated every social situation; seal 21 and 22 were socially submissive. Seal 3 behaved dominantly, except in the presence of seals 1, 2, 4, and 6.

Social rank was significantly correlated with roar duration ($r = 0.90$, $p < 0.0005$, Fig. 7); therefore, socially dominant males had longer roars than males with lower social status.

DISCUSSION

Characterization of underwater sounds produced by seals in a near shore, shallow water environment is complicated by multi-path sound propagation. Specifically, as sound travels from seal to hydrophone, the wave path propagates by bouncing off the surface or bottom of the ocean, or both as in reverberation (Fig. 8). Consequently, underwater vocalizations received by the hydrophone are distorted. Sound waves bouncing off the surface reverse phase and destructively interfere or mask sound at specific frequencies, whereas sound waves deflecting off the bottom constructively interfere or increase energy or loudness. Multi-path sound propagation, therefore, may have contributed to the significant spectral differences I observed in an individual's underwater vocalizations with respect to orientation. A seal's distance or depth also may affect sound propagation, as may environmental factors such as substrate composition, topography, and surface waves.

Harbor seals produce calls by contracting and expanding throat, thoracic, and chest areas, creating a turbulent flow of air through a constriction in their airway. The resulting sound is an aperiodic, flat-spectrum sound with broad frequency bands called formants. This contrasts with periodic sound, or harmonics produced by vibration of vocal cords. The first formant (F_o) was the most reliable and conservative measure of sound frequency in this shallow water environment. Although I did not measure significant frequency differences between each pair of adult males, individual identification may be possible with better quality underwater recordings from a stationary, bottom-mounted hydrophone beyond the surf zone and shallow water environment.

Regardless of limitations associated with recording in shallow water, I documented a relationship between social behavior and underwater vocalizations. Characteristics of vocalizations are presumably related to health, size, and experience of the individual. Specifically, sound production apparatus affects acoustic

output such that animals with long vocal tract lengths produce vocalizations with low formant frequencies (Fant 1960). Large, healthy, experienced males, therefore, may be able to produce longer, lower frequency vocalizations than other males. During this study, when male seals produced longer, deeper roars, nearby males responded by approaching and submissively posturing muzzle to muzzle with the roaring seal, indicating that seals may use acoustic cues to communicate social status and mediate social dominance hierarchies.

Further evidence regarding the role of underwater vocalization displays in establishing and maintaining social hierarchy among males included (1) observed difference in social behavior between attended and lone roaring males, (2) strong correlation between vocalization characteristics, such as duration and sound frequency, and social behavior, and (3) high ranking males had longer roars than males with lower social status. To summarize, socially dominant seals spent more time displaying [SPg and RW] within social groups than sparring or rolling [RO] with other males, presumably because their social rank was uncontested. In contrast, lower status males rolled [RO] with other seals and displayed when alone [RU and SPs] more frequently than dominant males because these males were more vulnerable to social contests with other males during underwater vocalizations. Behavioral differences were directly related to an individual's social status and acoustic cues (e.g. roar duration and frequency), indicating that seals may assess fighting ability or status based on underwater vocalization displays, then respond by contesting or attending a roaring seal, depending on their own social rank or potential risk of injury during sparring. Roar duration was a more reliable indicator of social rank than roar pitch presumably because call pitch may be distorted in a shallow water environment. In addition, males may not use roar pitch as a sole means of assessment but in combination with other physical traits, behavioral cues, or vocalization characteristics, because call pitch generally is related to body size, remaining constant after males are fully-grown, aged, and declining in fighting ability or social rank (Clutton-Brock and others 1979). Assessment of social rank or fighting ability based on vocalization characteristics also is evident among canids (wolf *Canus lupus*, Harrington and Mech 1979), cervids (red deer *Cervus elaphus*, Clutton-Brock and Albon 1979) and primates (howler monkey *Alouatta seniculus*, Sekulic 1982). Male

vocalizations, therefore, may function to maintain social hierarchy, reducing aggression or community instability by allowing males to assess each other before initiating a contest that could lead to serious injury.

In determining social hierarchy of male harbor seals within this community, dominance relationships among highest and lowest ranked males were clearly defined, whereas social relationships among closely ranked seals were less evident. This may be due to several factors. First, I did not observe social interactions among all possible seal dyads or pairings because as seals come and go from resting areas, chances of observing all possible pairs engaged in social activity were unlikely. This social hierarchy also may reflect relatively stable social relationships where contests are rare, aggression low, and individuals may actively avoid one another to prevent potential confrontations. In addition, social relationships among pairs of seals may vary depending on social context or presence of other seals that form temporary alliances to intimidate competition (chimpanzees, Goodall 1986; lions, Schaller 1972). Finally, direct competition for resources among these males, except during mating, is probably slight and may not warrant stringent linear social hierarchy characteristic of other social mammals. Clear dominance relationships among highest and lowest ranking males, however, indicated social hierarchy, which may play a significant role in determining male reproductive success.

Dominance hierarchies have been documented in a variety of social mammals including primates (chimpanzees *Pan troglodytes*, baboon *Papio* sp.), canids (wolf, hyaena *Crocuta* sp.), and felids (lion *Panthera leo*, Dewsbury 1982). Social status may explain variation in reproductive success by determining ease of access to mates. Reproductive success of high-ranking males, however, may not correlate directly with copulatory behavior. Benefits from social dominance may also include preferential access to resources such as food and shelter, as well as freedom from stress during social encounters. In studies of harbor seals, seasonal mating success does not vary significantly among males (Coltman and others 1999). Male harbor seals, however, exhibit preferential access to resting sites ashore and demonstrate social behavior based on social status, which may reduce aggression and ease stress among individuals within this community. These factors may increase

an individual's reproductive lifespan, enhancing fitness, although copulatory behavior within a season may not reflect greater reproductive success (Dewsbury 1982).

Future studies will focus on investigating how social status and underwater vocalization characteristics relate to overall reproductive success within this community. In addition, with improved acoustic monitoring capabilities, we will investigate how this communication of fitness or social status is relevant to mate selection. Specifically, we will record harbor seals in deeper water to avoid problems with multi-path sound propagation and obtain more reliable measures of sound frequency of individual seals. Further, we will extend the area where we record to monitor frequency, distribution, and social interactions among these individuals. These acoustic monitoring capabilities coupled with extensive knowledge of individuals within this community are well suited to address questions regarding the role of sound in the reproductive strategies of harbors seals; specifically, how seals develop and use underwater vocalization displays for communication, and how this process relates to mate selection and success.

Table 1. Summary of t-tests comparing underwater vocalizations of lone (2,4,6,7,10,12) and attended (15,16,17) males. Measurements include mean duration (s) of each call type (preroar, step, roar), total duration (preroar + step + roar) of underwater vocalizations, proportional duration of preroars, steps, and roars; and first formant frequency (F_0, Hz) of roars.

	Lone seals (2,4,6,7,10,12) Mean ± SE	Attended seals (15,16,17) Mean ± SE	df	t	p
Preroar (s)	2.0 ± 0.2	1.7 ± 0.1	9	0.87	0.41
Step (s)	**1.1 ± 0.2**	**0.3 ± 0.2**	**9**	**2.44**	**<0.05***
Roar (s)	**2.0 ± 0.1**	**3.3 ± 0.1**	**9**	**6.18**	**<0.00***
Total (s)	5.1 ± 0.2	5.3 ± 0.1	9	0.51	0.62
Preroar / Total	0.36 ± 0.04	0.30 ± 0.01	9	0.98	0.36
Step / Total	**0.23 ± 0.04**	**0.06 ± 0.03**	**9**	**2.74**	**<0.03***
Roar / Total	**0.42 ± 0.02**	**0.64 ± 0.03**	**9**	**7.62**	**<0.00***
Formant Frequency (F_0, Hz)	**223.7 ± 8.2**	**184.3 ± 5.1**	**9**	**3.17**	**<0.02***

Figure 1. Underwater vocalization behavior: (a) ignored roaring adult male [RA], (b) roaring male (indicated by arrow) with one adult male attending or maintaining passive muzzle or whisker contact [RW], and (c) roaring male (arrow) with five attending seals [RW].


a
b
c
1
2
3
4
5

Figure 2. (a) Spectrogram of male harbor seal underwater vocalization with preroar, step, and roar. The spectrum (b) represents a vertical slice of the spectrogram roar with frequency (kHz) along the horizontal axis and relative loudness (dB) along the vertical axis. The lowest peak frequency is the first formant frequency (F_0).

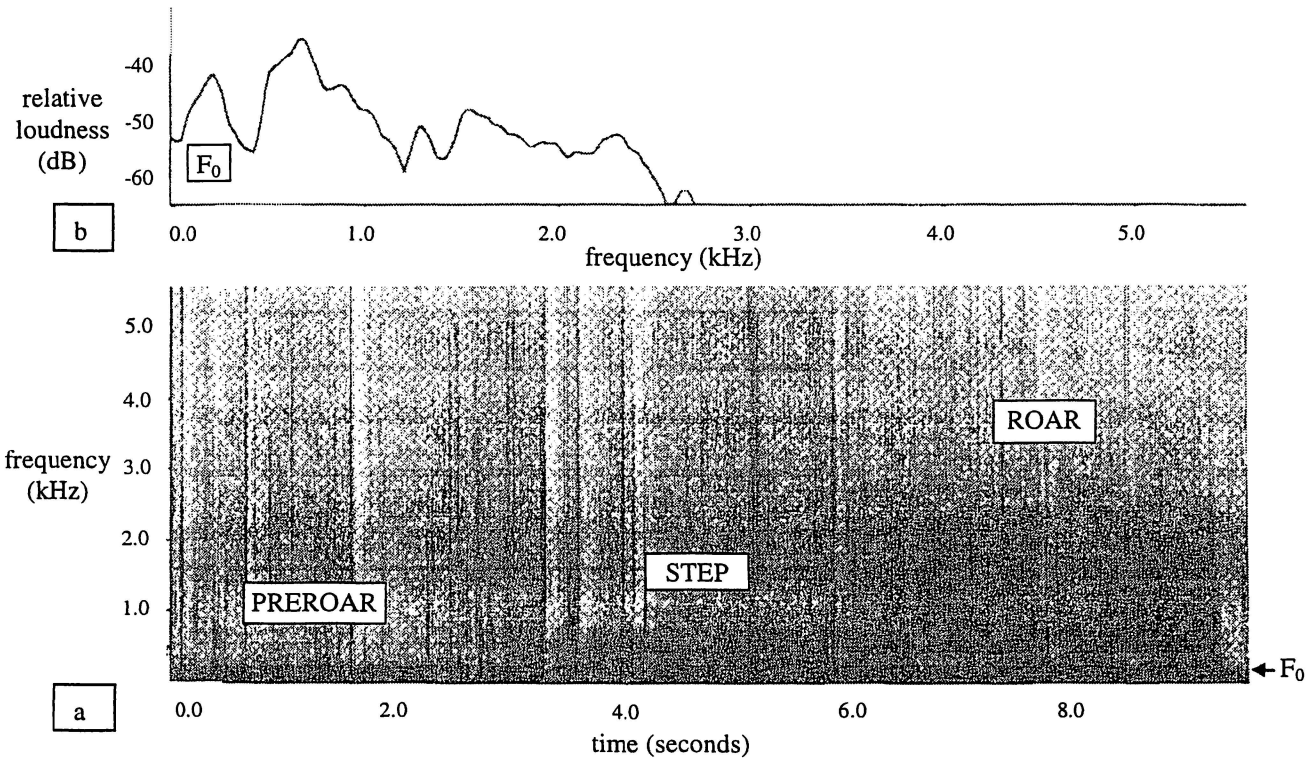

relative
loudness
(dB)
-40
-50
-60
F0
b
0.0
1.0
2.0
3.0
4.0
5.0
frequency (kHz)
frequency
(kHz)
5.0
4.0
3.0
2.0
1.0
ROAR
STEP
PREROAR
F0
a
0.0
2.0
4.0
6.0
8.0
time (seconds)

Figure 3. Joint distribution of mean roar frequency (F_0) ± SE and mean roar duration ± SE for lone (12,14,16,18,19,22), attended (1,2,3), and occasionally (20-35%) attended (5,6) seals. Attended males had longer and deeper roars than lone males. Roar characteristics of occasionally attended males fell between these two groups as indicated by the diagonal lines (lone males above the top line, attended males below the lower line).

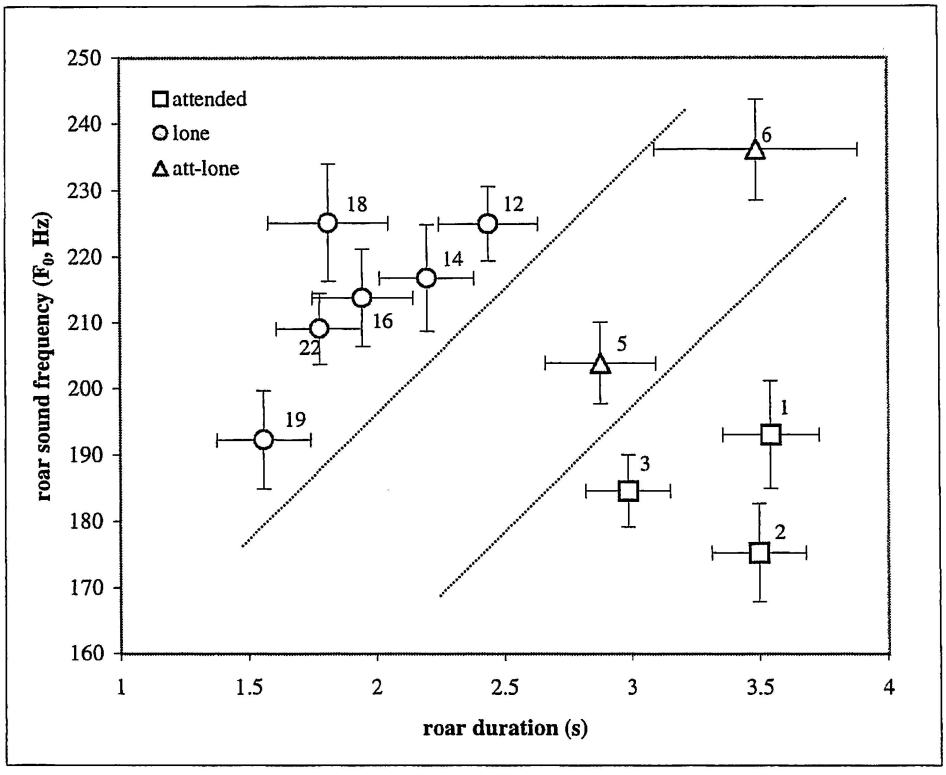

attended
lone
att-lone
250
240
230
220
210
200
190
180
170
160
1
1.5
2
2.5
3
3.5
4
roar sound frequency (F_0, Hz)
roar duration (s)
18
12
14
16
22
19
6
5
1
3
2

Figure 4. Factor scores for attended (1, 2, 3, 4, 5, 6) and lone (8, 12, 13, 14, 15, 16, 17, 18, 19, 22, 23) roaring males based on underwater behavior (roaring [RU], rolling [RO], flipper splashing in a group [SPg], attending [AT]). Frequency of attendance during roaring is indicated in parentheses below the seal ID number. Underwater vocalization displays [RU], RO, SPg, and AT were correlated (-0.83, 0.64, -0.62, 0.51) with factor 1 scores. Attending [AT] and RO were correlated (0.85, -0.75) with factor 2 scores. Factor 1 scores indicate significant differences in underwater behavior of attended and lone-roaring males.

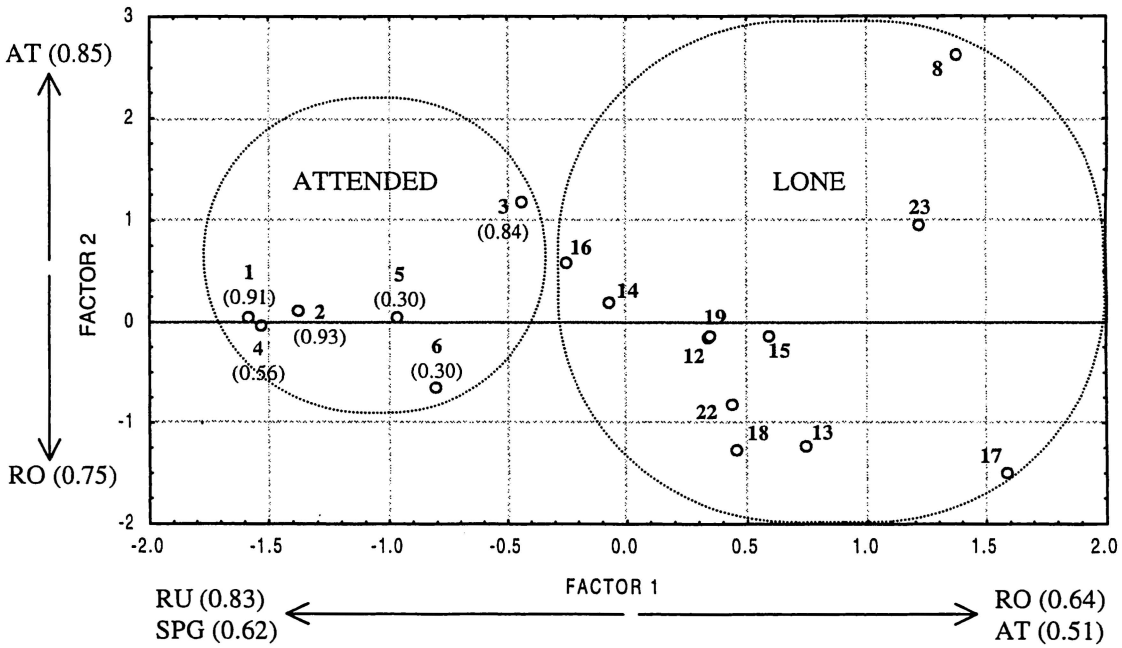

AT (0.85)
RO (0.75)
FACTOR 2
ATTENDED
LONE
1 (0.91)
2 (0.93)
3 (0.84)
4 (0.56)
5 (0.30)
6 (0.30)
8
12
13
14
15
16
17
18
19
22
23
FACTOR 1
RU (0.83)
SPG (0.62)
RO (0.64)
AT (0.51)

Figure 5. Canonical scores comparing underwater behavior (roaring while attended [RW], flipper splashing in a group [SPg]) and roar characteristics [RUD = duration (s), RUF = frequency (F_0, Hz)] of individual adult males (each seal numbered).

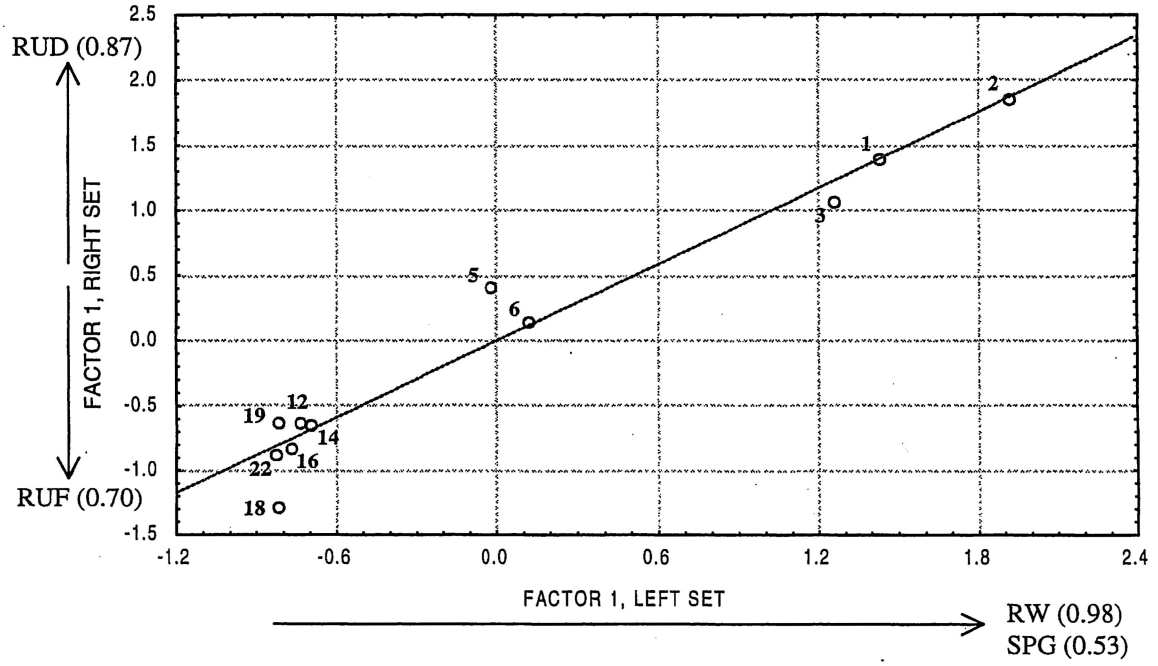

RUD (0.87)
FACTOR 1, RIGHT SET
RUF (0.70)
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.2
-0.6
0.0
0.6
1.2
1.8
2.4
FACTOR 1, LEFT SET
RW (0.98)
SPG (0.53)
1
2
3
5
6
12
14
16
18
19
22

Figure 6. Theoretical social hierarchy among adult males based on skew symmetry analysis of an asymmetrical matrix representing wins and losses between pairs of seals during social interaction. The result is a polar coordinate plot in which greater angle (radians) indicated greater dominance or social status, hence seal 1 is most dominant. Distance from the vertical center line (dotted) indicated deviation from a linear social dominance hierarchy.

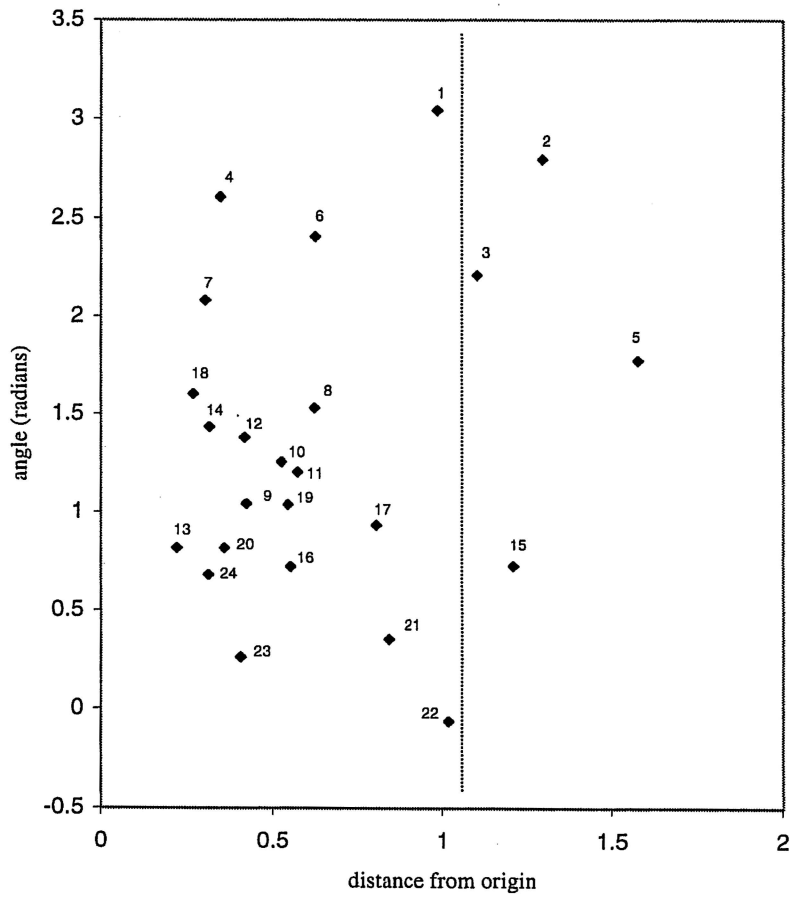

3.5
3
2.5
2
1.5
1
0.5
0
-0.5
angle (radians)
0
0.5
1
1.5
2
distance from origin
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24

Figure 7. Comparison of social rank and roar duration of eleven male harbor seals (1, 2, 3, 5, 6, 12, 14, 16, 18, 19, 22).

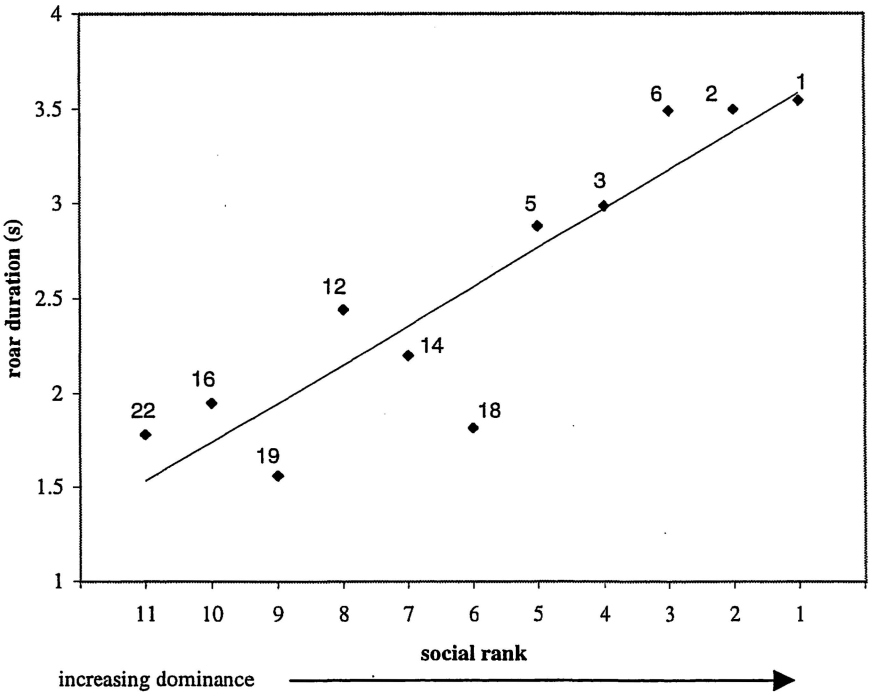
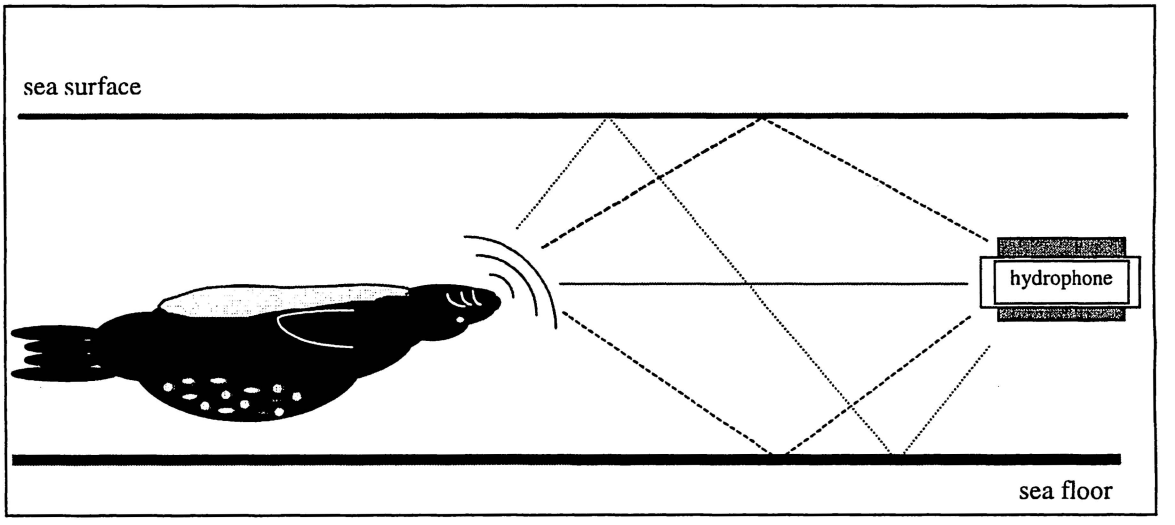

4
3.5
3
2.5
2
1.5
1
roar duration (s)
1
2
3
5
6
12
14
16
18
19
22
11
10
9
8
7
6
5
4
3
2
1
social rank
increasing dominance

Figure 8. Multi-path sound propagation of harbor seal vocalizations in shallow water.


sea surface
hydrophone
sea floor

CONCLUSION

Social and mating strategies among harbor seals may differ depending on habitat or access to ephemeral resources within the environment (Bartholomew 1970, Le Boeuf 1991). Harbor seals in southern Monterey Bay during 1995-1997 experienced extremely favorable environmental conditions, such as high oceanographic productivity, abundant prey, and low gill-net fishery effort. These conditions persisted for several years, resulting in community stability, characterized by fine-scale geographic fidelity, formation of long-term associations, a highly social underwater disposition, and social hierarchy. Individual patterns of behavior and social strategies, however, varied. These observations when applied to mating strategy indicated that these individual harbor seals demonstrated a range of tactics when selecting mates including mate fidelity, dominance relationships, underwater territories, scramble tactics, and social alliances.

Mating strategy depends upon female distribution and abundance relative to males (Bartholomew 1970, Le Boeuf). Within this community, females were twice as abundant as males and dispersed along the rocky coastline during breeding. Opportunities for males securing multiple mates (polygyny), therefore, were favorable, and dominance relationships established among males during the year may have influenced individual breeding strategy, or when and where along the coastline individual males advertise their breeding condition by displaying underwater. Underwater vocalization displays seem to communicate fitness and social status, and probably among these seal, individual identity. Dominant males, therefore, may use underwater vocalization displays to secure, defend, or patrol areas nearest to female resting areas, increasing probability of intercepting potential mates. Less dominant males, in contrast, may listen, using acoustic cues passively to determine location of dominant individuals, and essentially scramble for position, taking advantage of fleeting opportunities to intercept females in the absence of stronger, more experienced males. This tactic avoids conflicts or challenges, which may result in intense physical contests or injury.

Physical contests resulting in injury, however, were rarely observed, indicating that dominance relationships among males were well established and maintained during long-term associations. The longest recorded association among adult males within this community was seven years. These seals know one another and

assess relative strength and social status throughout years of social encounters, a characteristic rarely attributed to harbor seals. Underwater social behaviors such as attending, sparring or rolling, and mounting provide primary means of maintaining social hierarchy, although social function of these behaviors also may include learning and social development related to vocalization production and discernment of cues relevant to social identity or status, or even copulation. These behaviors also may function to establish social alliances among males, which may enhance reproductive success by improving an individual's ability to avoid confrontations with rivals, and pursue females.

This study, however, is limited to the community in southern Monterey Bay. Whether or not this information can be extrapolated to describe other harbor seal communities will require similar studies of seals living in different geographic locations or environments. Their widespread distribution throughout the Northern Hemisphere, however, is strong evidence that harbor seals are highly adaptable and capable of complex and diverse strategies for survival and reproduction.

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